SPATIAL AND TEMPORAL AVAILABILITY OF PACIFIC SALMON MEDIATE COMPENSATORY GROWTH IN COASTRANGE SCULPIN AND SEX-AGE SPECIFIC SPATIAL HABITAT USE IN BROWN BEARS

By

Michael Joel Godin, B.A.

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APPROVED:

Dr. David Tallmon, Committee Chair
Dr. Megan McPhee, Committee Member
Dr. Sanjay Pyare, Committee Member
Dr. Gordon Kruse, Chair
Department of Fisheries
Dr. S. Bradley Moran, Dean
College of Fisheries and Ocean Sciences
Dr. Michael Castellini, *Dean of the Graduate School*

Abstract

Pacific salmon bring marine nutrients into freshwater ecosystems and provide food for countless species. Two major consumers of salmon along the Pacific coast are Coastrange Sculpin *Cottus aleuticus* and brown bears *Ursus arctos.* I examined the effects of salmon temporal availability on the growth rate of sculpin and the spatial use of habitat by brown bears.

In a study on Coastrange Sculpin I found that treatment groups denied food, in the form of salmon eggs, for two or three weeks exhibited compensatory growth following resumption of feeding in the laboratory and field respectively. The compensatory growth response was mediated by stream of origin and temperature, controlled in the laboratory. Sculpin groups from different streams of origin had different overall growth rates in the laboratory despite being housed under identical conditions. At the end of the food-deprivation period, sculpin housed at 20°C exhibited a 5% greater weight loss compared to sculpin housed at 10°C. High temperatures (20°C) prevented compensatory growth in one treatment group and lengthened the catch up period for other treatment groups compared to those housed at moderate temperatures (10°C).

In a study on brown bear spatial and temporal use of habitat in Berners Bay, Alaska, I found that brown bears use salmon when they are available and reproductive status of adult female bears affects use of this resource. Brown bears used space within 250 meters of salmon spawning reaches 50% more when salmon were present (69%) than when salmon were not present (19%) at spawning reaches. However, sex, age, and reproductive status all affected the use of space near spawning reaches. When salmon were available, adult females without cubs used space similarly to dominant adult males, while females with cubs used space similarly to subdominant juveniles. Adult females without cubs used space within 100 meters of spawning reaches 13% more than females accompanied by cubs.

Salmon runs in Southeast Alaska are exhibiting reduced duration and earlier arrival of migration timing, reducing their temporal availability to consumers. Additionally, climate change is projected to increase temperatures throughout Southeast Alaska. Warmer temperatures resulting from climate change may improve digestion and growth for sculpin in colder streams, but could negatively affect the ability of sculpin to exhibit compensatory growth. Reduced salmon availability and increased human activity might lead to changes in behavior and dominance among brown bears feeding on salmon.

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General Introduction

Pacific salmon *Oncorhynchus* spp. are one of the most intensely studied genera of fish and include a variety of unique life histories throughout the members of the genus. Anadromous forms begin their lives in freshwaters from California to Alaska, and along the Pacific coast of Russia and Japan. Five species of anadromous salmon spawn along the Pacific coast of North America and feed in the cold, nutrient-rich waters of the North Pacific Ocean. Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka* together comprise over 90% of the total abundance (Quinn 2005) and total catch (Beamish and Bouillon 1993) from fisheries in the eastern and western Pacific. Chinook Salmon *O. tshawytscha* are the largest but least abundant of the five species found in North America (Quinn 2005). Coho Salmon *O. kisutch* abundance is intermediate to that of Chinook Salmon and the other three more abundant North American species (Quinn 2005). The anadromous life history of these salmon results in a vast quantity of marine derived biomass being transported into freshwater (Finney et al. 2000, Gresh et al. 2000, Naiman et al. 2002). Anadromous salmon can put on over 99% of their body mass in the marine environment and this biomass is transported back to freshwaters during the spawning migration (Quinn 2005). This transport of marine biomass can drastically alter the freshwater ecosystems through pulsed food subsidies of adult salmon and their eggs (Chaloner et al. 2007, Armstrong et al. 2010, Rinella et al. 2012, Armstrong and Bond 2013, Armstrong and Schindler 2013, Swain et al. 2014, Swain and Reynolds 2015).

Pacific salmon are a prey item for a myriad of predators throughout their life cycle. Fry and migrating smolts are consumed by stream fishes during their residence in freshwaters and seaward migration (Ruggerone and Rogers 1992, Anderson et al. 2005, Tabor et al. 2007). Juvenile salmon are thought to experience two major sources of mortality during the first year at sea. The first period of high mortality is due to predation, with decreasing mortality as the juvenile salmon rapidly outgrow the gape limitation of many predators (Beamish and Mahnken 2001). The second period of mortality comes during winter when food items are less plentiful, and some individuals starve (Beamish and Mahnken 2001). As salmon continue to grow in the marine environment, they fall prey to large predators such as Salmon Sharks (*Lamna ditropis;* Nagasawa 1998), killer whales (*Orcinus orca*; Ford et al. 1998, Saulitis et al. 2000, Ford and Ellis 2006), and pinnipeds (suborder Pinnipedia; Nehlsen et al. 1991, Zamon 2001). Salmon reach sexual maturity in 1-7 years depending on species and individual growth characteristics

(Quinn 2005). On the return journey to their natal spawning grounds, adult salmon are harvested by commercial fishing fleets comprised of gill netters, seiners, and trollers. Each of these human predation methods puts a different kind of selective pressure on the returning stock, potentially affecting the diversity of the adults that make it to the spawning grounds (Ricker 1981, Heino and Godo 2002, Hard et al. 2008). Once the returning stock has reached their natal stream system, they are preyed upon by terrestrial, avian, and aquatic consumers such as bears (Hilderbrand et al. 1999a, Quinn and Kinnison 1999, Gende et al. 2004, Deacy et al. 2016), seagulls (Mossman 1958, Quinn and Buck 2001, Schindler et al. 2013), and other carnivorous riparian predators (Ben-David et al. 1997). When salmon are actively spawning, sculpin (Dittman et al. 1998, Foote and Brown 1998, Swain et al. 2014, Swain and Reynolds 2015), resident salmonids (Armstrong et al. 2010, 2013, Quinn et al. 2012, Rinella et al. 2012, Armstrong and Schindler 2013), and other stream fishes consume large amounts of salmon eggs and the flesh of senescent adults. Despite salmon being available for only a few months each year, the pulsed subsidy of salmon eggs and flesh provides a food source that allows increased growth (Foote and Brown 1998, Quinn et al. 2012), and higher population densities (Hilderbrand et al. 1999b) of predators that might otherwise be limited by food availability.

Over the last century the North Pacific Ocean has undergone several oceanographic regime shifts, which have affected abundance of salmonid species throughout their range. A period of high ocean productivity gave way to a low productivity period around 1947, which reversed back to high productivity around 1977, lasting until approximately 1990 (Mantua et al. 1997, Irvine and Fukuwaka 2011). From 1990 onward, populations of Pink Salmon, Chum Salmon, and Sockeye Salmon maintained relatively high productivity, while Chinook Salmon and Coho Salmon have gradually declined in total abundance (Irvine and Fukuwaka 2011). In addition to changes in abundance, many salmon stocks have experienced decreased size-at-maturity since the regime shift in the late 1970s possibly related to fishing, inter and/or intraspecific density dependence in the ocean (Ruggerone and Connors 2015), or other environmental factors (Bigler et al. 1996).

Over the last 50 years, several populations of salmon have changed their migration timing in Southeast Alaska. Many Stocks of Pink Salmon, Chum Salmon, and Coho Salmon throughout Southeast Alaska are arriving at freshwater systems earlier in the year. Those stocks that show the greatest change in mean spawning date also have the greatest decreases in duration of

spawning (Kovach et al. 2015). Climate change and associated warming stream temperatures have been associated with changes of earlier spawning migration date, and reduced duration of migration timing in several salmonid species (Kovach et al. 2012, 2013). Earlier and shorter spawning migrations reduce the availability of salmon to consumers in the freshwater environment relying on salmon as a dependable food source.

In Southeast Alaska, two consumers that rely heavily on the pulsed food subsidy of spawning salmon are Coastrange Sculpin *Cottus aleuticus* and brown bear *Ursus arctos*. These species are on opposite ends of the salmon consumer size spectrum and consume large amounts of adult salmon flesh and eggs. Coastrange Sculpin are a small benthic fish species that can be found along the Pacific coast from California to the Aleutian Islands. During salmon spawning, sculpin gorge themselves on salmon eggs and exhibit increased body condition due to this abundant food source (Foote and Brown 1998). The salmon egg subsidy is temporally limited however, and sculpin must consume as many eggs as possible while they are available. Brown bears in North America are found throughout northwestern Canada and Alaska, but subspecies are abundant throughout Eurasia as well. Coastal brown bear populations feed on salmon during much of the summer and can track unique runs of salmon across a landscape in order to maximize the number of days spent feeding (Schindler et al. 2013, Deacy et al. 2016). Earlier spawning date and shorter spawning duration of salmon populations in Southeast Alaska might affect how sculpin and bears use these salmon food subsidies.

In Chapter 1, I examine the growth of Coastrange Sculpin when fed a diet of salmon eggs in both field and laboratory experiments. The objective of this study was to determine if Coastrange Sculpin are capable of exhibiting compensatory growth when given a temporally limited diet, and to examine the role of temperature on growth rates. In Chapter 2 I examine the spatial and temporal use of space by brown bears in Berners Bay near Juneau, Alaska. The objective of this study was to determine if these brown bears use salmon as a food source, if sex and age affects this use, and if reproductive status influences how adult females use salmon food subsidies.

My study area is Berners Bay and the greater Juneau area in Southeast Alaska. This area is host to four naturally occurring species of Pacific salmon, which are available from mid-July through October. Streams systems in this area range from entirely rain-fed to heavily glacier-fed and thus differ markedly in thermal regimes as well as the timing and extent of salmon

occurrence. The influence of glaciers, snowpack, summer precipitation, and changes in these characteristics due to climate change all affect the temperature of different stream systems used by salmon, Coastrange Sculpin, and brown bears.

These two studies of salmon consumers fit into the Alaska Experimental Program to Stimulate Competitive Research or Alaska EPSCoR. This program provided partial funding for this research, and funds many other projects that study organisms and habitats from the ice fields to the estuary in Southeast Alaska. My studies might also be useful in describing the effects of climate change on consumers relying on salmon. The study on Coastrange Sculpin explicitly examines how increased temperatures impact the sculpin growth rates when feeding on salmon eggs. In addition, these studies provide insight into how changes in salmon spatial and temporal availability due to climate change might impact Coastrange Sculpin and brown bears if climate change continues as projected.

Chapter 1: Coastrange Sculpin *Cottus aleuticus* Exhibit Compensatory Growth When Provided a Temporally Limited Diet of Salmon Eggs, a Response Mediated by Temperature.

Abstract

Coastrange Sculpin *Cottus aleuticus* are a major consumer of salmon eggs and rely heavily on this pulsed food source. Whether Coastrange Sculpin are capable of undergoing compensatory growth to further capitalize on this temporally limited abundance has not yet been tested. Using both field and laboratory experiments, this study examines whether Coastrange Sculpin can undergo compensatory growth when given a temporally limited diet of salmon eggs and how temperature affects this growth. Control groups were fed *ad libitum*, while treatment groups were denied food for the first two (laboratory) or three (field) weeks before being fed *ad libitum*. The percent change in weight was used to identify compensatory growth in the treatment groups. I predicted that sculpin would exhibit compensatory growth in the field under natural conditions and in the laboratory at a moderate temperature of 10°C, but not when housed in the laboratory at 20°C, which is relatively high for streams in Southeast Alaska. In the field, treatment groups at all three streams exhibited compensatory growth. In the laboratory, treatment groups from four streams of origin exhibited compensatory growth when held at 10°C. Three out of four treatment groups from unique streams exhibited compensatory growth at 20°C, but the response was suppressed compared to their stream site counterparts held at 10°C. Elevated temperatures increased overall growth rates, but prolonged the time period needed for treatment groups to catch up with their respective controls. This study demonstrates that Coastrange Sculpin are capable of undergoing compensatory growth when provided a temporally limited diet of salmon eggs and that warmer temperatures can increase growth, but suppress food limited individuals.

Introduction

Many species of fish regularly undergo or have the ability to undergo periods of accelerated growth during favorable conditions following a period of growth depression, known as compensatory growth (Ali et al. 2003). Compensatory growth can occur when an individual

[1]Godin, M. and D. Tallmon. 2017 Coastrange Sculpin Cottus aleuticus exhibit compensatory growth when provided a temporally limited diet of salmon eggs, a response mediated by temperature. Prepared for submission to Transactions of the American Fisheries Society.

experiences a period of limited nutritive intake, followed by a period of substantially greater nutritive intake. The most common cause of compensatory growth is limited availability or quality of food followed by a period where food is extremely abundant or of greater nutritive quality (Weatherly and Gill 1981, Ali et al. 2003). In addition, a change in temperature (Nicieza and Metcalfe 1997), oxygen levels (Foss and Imsland 2002), and other environmental conditions (Ali et al. 2003) stimulate compensatory growth in some species. Compensatory growth allows nutritionally repressed individuals to catch up with their cohort in terms of length and/or weight. However, compensatory growth may in some cases have negative long term survival and fecundity consequences (Johnsson and Bohlin 2005, Mangel and Munch 2005), though these consequences are not well understood and vary by species.

In Southeast Alaska, Pacific salmon *Oncorhynchus* spp. fry emerge from the gravel and emigrate throughout spring (Holtby et al. 1989) with the majority of smolts having left freshwaters for the marine environment by mid-May (Kovach et al. 2014). Adult salmon generally return to spawn in mid to late summer, several months after the outmigration of smolts. Resident stream fishes must endure many weeks of relatively poor feeding conditions (Wipfli et al. 1998, 2003, Wipfli and Gregovich 2002) between the emigration of smolts and the arrival of adult spawning salmon. Additionally, some salmon populations in Southeast Alaska show decreasing temporal duration of their spawning runs over the last few decades (Kovach et al. 2012, 2013) further restricting the temporal availability of salmon eggs to sculpin. However, during those few weeks of egg availability, consumers are presented with a highly nutritive and often abundant food resource. This scenario of low food availability followed by abundant and calorically dense food is consistent with conditions that result in compensatory growth in other fish species (Jobling et al. 1993, Hayward et al. 1997, Ali et al. 2003).

Coastrange Sculpin *Cottus aleuticus* are a small benthic fish species that inhabit stream, lake, and brackish water habitats from California to the Aleutian Islands. They are prey for resident salmonids (Moyle 1977), as well as other aquatic, avian, and terrestrial consumers. Sculpin are opportunistic sit-and-wait type predators, feeding on invertebrates, small fishes, and salmonid eggs (Swain et al. 2014). In some systems sculpin can derive a substantial portion of their annual nutritive intake from pulsed subsidies of salmon fry and eggs (Kline et al. 1993).

Whether Coastrange Sculpin are capable of undergoing compensatory growth has not yet been experimentally examined. Some evidence of rapid growth was observed at Iliamna Lake,

where sculpin gather in large numbers to prey on salmon eggs in nests of beach spawning Sockeye Salmon *O. nerka*. Sculpin were in poor condition before the arrival of salmon, but increased substantially in weight over the course of the short salmon spawning season (Foote and Brown 1998). The spawning season in Iliamna Lake lasts only 1-3 weeks, providing a very brief window for sculpin to exploit this pulsed resource.

In Southeast Alaska, the majority of freshwater habitat is comprised of glacier- or rain-fed streams. These two stream types are fundamentally different from one another in terms of temperature and flow regimes. Rain-fed streams have a temperature profile that closely matches that of ambient air, with warm summer temperatures and cold winter temperatures, whereas glacier-fed streams do not match the temperature profile of ambient air, having colder temperatures in summer from glacial melt with high ambient air temperatures (Fellman et al. 2014). The temperature of a glacier-fed stream may vary as little as 5°C over a yearly cycle, whereas rain-fed streams can vary by 20°C or more over the same period.

Temperature plays a large role in digestion rates of ectotherms like Coastrange Sculpin, affecting how quickly they can assimilate and continue to feed. When the aquatic habitat has localized temperature heterogeneity, other sculpin and salmonid species exhibit diel migrations from cold waters where food is more abundant to warmer habitats to increase the rate of digestion (Neverman and Wurtsbaugh 1994, Armstrong and Schindler 2013, Armstrong et al. 2013). The increased rate of digestion via temperature can be accompanied by an increase in gut blood flow to remove waste and increase nutrient absorption (Eliason et al. 2008, Gräns et al. 2009, Gräns et al. 2013) in addition to gut and digestive plasticity (Armstrong and Bond 2013).

Temperatures higher than what is optimal for digestion negatively impact growth through increased basal metabolism and physiological stress (Handeland et al. 2008, Neuheimer et al. 2011, Crozier and Hutchings 2014). The final thermal preferendum temperature for a species is a function of metabolic efficiency and a balance of other physiological processes specific to that species (Jobling 1981). A study on Slimy Sculpin *C. cognatus* found avoidance behavior, upper lethal, and final thermal preferendum temperatures to be approximately 18°C, 26.5°C, and 10°C respectively (Otto and Rice 1977).

The objectives of this study were to experimentally examine whether Coastrange Sculpin are able to undergo compensatory growth when given a temporally limited diet of salmon eggs, and to explore the effects of temperature on growth in sculpin from glacier- and rain-fed streams.

A field experiment where sculpin were housed in their native stream examined differences in the compensatory growth response of Coastrange Sculpin from streams that vary in temperature and glacial influence. A laboratory experiment explored the influence of experimentally increased temperature on the compensatory growth response in Coastrange Sculpin from four rain-fed or glacier-fed streams. I hypothesized that Coastrange Sculpin would exhibit compensatory growth when fed salmon eggs to the point of satiation after undergoing a period of restricted caloric intake (1) in their native stream and (2) in the laboratory at a moderate temperature of 10°C, (3) but compensatory growth would be inhibited in the laboratory at a high temperature of 20°C.

Methods

The Coastrange Sculpin used in this study were from four Juneau area streams (Fig. 1) across a gradient of thermal regimes. Auke Creek is a rain-fed system that flows 0.5 km from Auke Lake into the ocean. It has the warmest temperature regime of the four stream sites, with summer temperatures exceeding 20°C in recent years. Salmon Creek is entirely rain-fed, but flows out of the Salmon Creek Reservoir giving it a colder temperature profile compared to Auke Creek, averaging 10°C during summer. Cowee Creek has moderate glacial influence averaging 7°C during the summer months. Coastrange Sculpin from these three sites were used for both the field and laboratory experiments. Along with these three streams, sculpin from the Mendenhall River were used exclusively in the laboratory experiment. The Mendenhall River is a glacier-fed stream with a relatively constant temperature of approximately 3°C during the summer months. These streams not only vary in their summer temperatures, but in their annual temperature regime patterns relating to their percentage of glacier or rain inputs (Fig. 2). The temperature regimes and freshwater inputs of these four streams are representative of the streams found in the Juneau area and throughout much of Southeast Alaska (D. L. Chapman, 1982 NOAA Technical Memorandum NWS AR-35, U.S. Department of Commerce, on daily flow statistics of Alaskan streams, Fellman et al. 2014, Shanley et al. 2015)

Field Experiment

In the field experiment, enclosures were constructed from 30.5 cm lengths of 10 in (25.4 cm) diameter PVC pipe with ¼-in (0.6 cm) vinyl coated wire mesh covering both openings. Two ¾-in (1.9 cm) stainless steel conduit straps were attached to the enclosure exterior to hold rebar stakes and a hatch was cut into the PVC to allow access to the enclosure during the experiment. These enclosures were partially filled with gravel and rocks from their respective streams sites

and staked to the stream bed with the openings facing the current. The enclosures were set up in two columns of five with approximately 1 meter separating enclosures both within and between columns (Fig. 3).

Coastrange Sculpin were captured using kick nets and minnow traps baited with salmon eggs (Dittman et al. 1998). Sculpin were placed directly into enclosures at their respective streams upon being captured and held there until approximately 60 individuals were collected. Sculpin were promptly returned to the stream if they were smaller than 70 mm to ensure that all sculpin used in the experiment would be large enough to consume eggs from Chum Salmon *O. keta* (Armstrong et al. 2010), which are abundant in Juneau area streams and were the salmon egg source used in this study. To control for the potentially confounding effect of body size, the 20 largest sculpin were selected and randomly assigned to enclosures. In the first row, the enclosure in the first column was randomly assigned as either control or treatment diet. The enclosure in the second column was assigned as its complement. Each successive row alternated this pattern of control and treatment so that any differences in hydrodynamics were equally applied to both groups. To maintain a balanced sample size among stream sites while allowing for mortalities during the experiment, two sculpin were housed in each enclosure and received the same treatment. To keep fish densities equal among enclosures, any mortalities were replaced by a new sculpin with a pectoral fin clip denoting that it could not be used for the analysis. The field experiment was conducted at the three stream sites, Auke Creek, Salmon Creek, and Cowee Creek, in parallel from June through September. The enclosures at Cowee Creek were placed in the confluence of Cowee Creek and one of its glacier-fed tributary streams Davies Creek. All sculpin used at this site were captured in the main stem of Cowee Creek.

Weight data were recorded for each Coastrange Sculpin on the first day of the experiment and control enclosures were provided with 25 Chum Salmon eggs. Salmon eggs were collected from culled hatchery Chum Salmon at the Auke Creek weir and frozen for use in both the field and laboratory experiments. Fresh salmon eggs were provided twice weekly, and old eggs were cleaned out as needed during the experiment. Salmon eggs were observed among all enclosures between feeding periods and were continuously available to the sculpin, ensuring *ad libitum* feeding. Control sculpin were fed *ad libitum* for the duration of the experiment. Treatment enclosures were denied salmon eggs for three weeks during the food deprivation period. The ¼-in (0.6 cm) vinyl-coated wire mesh limited the flow of items into the enclosures, specifically

naturally spawned salmon eggs. After three weeks the treatment food deprivation period ended and all enclosures were fed *ad libitum* with twice weekly feedings of 25 salmon eggs. Weight data were collected for all individuals at the start of the experiment, again at week 2, at week 3 before feeding the treatment group, and every two weeks thereafter until the end of the experiment at week 11. Weight data were collected at the end of the experiment and all individuals were returned to their native stream.

Laboratory Experiment

The laboratory experiment used Coastrange Sculpin from Auke Creek, Salmon Creek, Cowee Creek, and the Mendenhall River. The primary objective of this experiment was to examine how temperature affects compensatory growth in sculpin from rain-fed and glacier-fed streams. Based on preliminary field studies it was predicted that compensatory growth would be exhibited by fish housed in 10°C water and prevented in fish housed in 20°C water when fed salmon eggs *ad libitum* after a period of starvation. These two temperatures are characteristic of the study streams during normal summer temperatures (10°C), and during abnormally hot summers (20°C; Wing and Pella, 1998 NOAA Technical Memorandum NMFS-AFSC-91,90, U.S. Department of Commerce, on time series analysies of climatological records from Auke Bay, Alaska) which are becoming increasingly more common in Southeast Alaska.

Coastrange Sculpin for the laboratory experiment were collected in the same manner as for the field experiment. Sculpin were transported back to the laboratory in a 40 L rectangular tank equipped with a portable aerator. At the laboratory four 175 L tanks were set up with a 100 gal (378.5 L) rated water filter, a heating unit, tank mixer, and 12 in (45.4 cm) air stones connected to a 100 gal (378.5 L) rated air pump. To regulate the water temperature below ambient air temperature, the 175 L tanks were partially submerged in larger tanks equipped with flow through ocean water. The ocean water flowing around the 175 L tanks effectively cooled them to around 6°C and allowed the tanks to be heated to the experimental temperatures of 10°C and 20°C. The freshwater tanks were reliably heated to within 1°C of the desired temperature despite ambient air temperatures fluctuating around 18°C.

Smaller enclosures were made from rectangular plastic food containers approximately 20 cm long, 13 cm wide, and 8 cm tall. To allow for water circulation within each enclosure, 0.5 cm diameter holes were melted into the vertical side walls with approximately 2 cm spacing between holes. These enclosures were numbered and labeled with a stream name. The odd numbered

enclosures were assigned as controls and the even numbered enclosures were assigned as treatments. These small enclosures were lined with a thin layer of gravel taken from Salmon Creek as substrate.

During the collection period Coastrange Sculpin were housed in the freshwater tanks at 10°C, one tank for each of the four unique stream cohorts. The sculpin were given approximately a 3% of body weight maintenance ration (Chadwick and Brocksen 1969) consisting of frozen blood worms provided twice weekly during the collection and subsequent acclimation periods. After collection, sculpin within each stream cohort were randomly assigned to their respective enclosures. Each enclosure housed two sculpin, which allowed for mortalities while maintaining a balanced design among tanks, stream cohorts, and treatments. Each larger tank held 40 smaller enclosures with five control and five treatment enclosures per stream cohort. Two tanks were randomly assigned to the 20°C treatment and temperature was stepped up from 10°C to 20°C over 10 days, increasing the temperature by 1°C every 24 hours.

The enclosures were set up in eight vertical stacks that were five enclosures tall, alternating control and treatment enclosures in each stack. Every two days the stacks were rotated systematically through the tank, and the bottom enclosure from each stack was moved to the top. This was done to evenly distribute any possible spatial differences in dissolved oxygen, water chemistry, or hydrodynamics among enclosures. Water changes of approximately 70 L were conducted every two days. Stress Coat® water conditioner (API Fish Care), ammonia neutralizer, and aquarium salt for freshwater tanks were added with every water change to maintain healthy water quality.

Coastrange Sculpin in the control group enclosures were fed Chum Salmon eggs to the point of satiation twice weekly for the entire eight weeks of the experiment. The treatment group was completely deprived of food for two weeks (Hayward et al. 1997), followed by feeding with Chum Salmon eggs to the point of satiation twice weekly for the remaining six weeks. Weight data were taken for all individuals every two weeks throughout the experiment. In the first week of the experiment, the 25 Chum Salmon eggs were left in the control enclosures until the next feeding period when they were cleaned out and replaced with fresh eggs. However, the rapid breakdown of these eggs led to high levels of dissolved ammonia and poor water quality. In the second week of the experiment the feeding protocol was adjusted by reducing the number of eggs fed at each period, but ensuring that there was always a surplus after 24 hours. The

Coastrange Sculpin were then given 24 hours to feed *ad libitum* before the eggs were removed from all of the enclosures. This meant sculpin would be without food for a maximum of one or two days between feedings. Sculpin were nearly always observed with full stomachs, often with the outline of undigested eggs still visible two days after eggs had been removed from the enclosures. Since eggs were not continuously available the feeding regime was quasi *ad libitum*, but will be referred to as *ad libitum*. Any sculpin mortalities were removed and replaced with a healthy individual which was not included in the final analysis. If any enclosure experienced mortality during the experiment, the surviving individual was automatically assigned to the focal group. At the end of both experiments a focal individual was randomly selected from the surviving fish in each of the enclosures and only this individual was included in the final analysis. For both field and laboratory studies, each unique control or treatment group used in the final analysis had a sample size of five individuals.

The statistical analysis was conducted similarly for both the field and laboratory experiments and carried out in R 3.2.2. Coastrange Sculpin cohorts from each stream were composed of fish with different starting lengths and weights. Percent weight change (PWC) was calculated measuring the percent change in weight from the start of the experiment to every successive data collection period. For the range of sizes among the sculpin used in this study PWC scaled isometrically by size, thus effectively adjusting for the starting size of the individual. Starting weights for sculpin used in both field and laboratory analyses can be found in the supplementary material (Table S1). The PWC value was calculated at each time period using the equation $[(W_s-W_i)*100/W_i]$, where W_s is sample weight and W_i is initial weight (Dobson and Holmes 1984, Quinton and Blake 1990). The field experiment was analyzed with a three-way ANOVA with factors of stream, diet treatment, time, and their interactions. The laboratory experiment was analyzed with a four-way ANOVA with factors of stream, diet treatment, temperature treatment, time, and their interactions. After significant factors were identified for the field and laboratory ANOVA's, contrasts between control and treatment groups at each time period were conducted and a Bonferroni adjustment was applied. Compensatory growth was identified in a treatment group when the PWC values were not significantly different from their respective control group.

The ANOVA assumptions of constant variance and normality were assessed graphically and with the formal tests Fligner-Killeen (Conover et al. 1981) and Shapiro-Wilk (Shapiro and

Wilk 1965) respectively. The Fligner-Killeen test was selected over Bartlett's test to examine constant variance due to the small sample size and wide spread of the plotted points in the residual plots, though these two tests presented similar results in most cases. For both the field and laboratory experiments, the data showed a violation of the normality assumption. Since the PWC data has negative values for treatment fish during the food deprivation period, a constant value of 50 (percent) was added in order to centralize the data away from zero without negative values. A Box-Cox transformation (λ= -0.5) was used to normalize the data in both experiments.

In the laboratory experiment, three fish showed weight loss despite having regular access to salmon eggs, and their growth patterns were consistent with other individuals that had become sick and died during the experiment. These fish were from three unique groups (one individual each from a Mendenhall River control group held at 20°C, a Mendenhall River control group held at 10°C, and a Cowee Creek treatment group held at 20°C) indicating there was not a treatment diet, treatment temperature, or tank related affect. Removing the individuals did not meaningfully change the interpretations of the ANOVA or contrasts (data not shown) and the reported results are from the analysis with these fish removed. For all analyses, values were considered "significant" at a level $\alpha < 0.05$. Values at a level $\alpha < 0.10$ for the contrasts were considered "weakly significant" and were only used in conjunction with other significant results to make inferences.

Results

Field Experiment

In all three stream cohorts, food-deprived Coastrange Sculpin lost weight during the deprivation period and exhibited compensatory growth after resumption of feeding, attaining weights similar to their respective control groups by the end of the experiment. However, overall cohort growth was influenced by stream site where Auke, Salmon and Cowee Creek cohorts had the highest, middle, and lowest percent weight change (PWC) values, respectively, at the end of the experiment.

Coastrange Sculpin growth was significantly affected by stream, diet treatment, and time as well as the interaction of diet and stream (three-way ANOVA; Table 1). The significant stream effect indicates that there were stream-specific differences in the growth trajectories of sculpin irrespective of their diet treatment, and the significant diet treatment effect indicates that the restricted diet influenced the growth of each treatment group. The significant interaction of

both stream and diet indicate that in addition to stream site characteristics influencing growth, the effects of the treatment diet differed between stream cohorts.

After being deprived of food, the PWC values of treatment groups at each stream were significantly less than their respective control groups. Auke Creek, Salmon Creek, and Cowee Creek treatment groups remained significantly different from their respective control groups for the next six, four, and two weeks of *ad libitum* feeding, respectively, before catching up with their controls (Fig. 4; Table 2). At the end of the experiment, Coastrange Sculpin from Auke Creek had the greatest overall growth (75% increase), followed by Salmon Creek (50%) and Cowee Creek (42%).

Laboratory Experiment

All fish in diet treatment groups lost weight during the food deprivation period and increased in weight after being fed *ad libitum* regardless of temperature. Some, but not all, treatment groups exhibited compensatory growth by the end of the experiment. The treatment groups housed at 20°C experienced greater weight loss during the food deprivation period compared to their counterparts at 10°C. This led to a greater difference between treatment and control groups in the 20°C tank throughout the experiment and inhibited compensatory growth for some treatment groups at 20°C.

Growth of Coastrange Sculpin in the laboratory was significantly affected by diet, stream, time, and temperature (four-way ANOVA). Additionally, the two-way interaction terms of both diet and stream with temperature were significant, as well as the three-way interaction of diet, stream, and temperature (Table 1). The significant stream effect indicates that sculpin housed under identical conditions exhibit different growth trajectories based on stream of origin. The significant temperature effect indicates that there is a significant difference in the growth trajectories of the different groups at 10°C and 20°C. The significant two and three-way interaction terms of stream, diet, and temperature indicate that for these three factors any given factor has mediating effects on any other factor.

At 20°C three out of four diet treatment groups exhibited compensatory growth. All four diet treatment groups had significantly lower PWC values than their respective controls after two weeks of starvation. Auke Creek, Cowee Creek, and Mendenhall River treatment groups all exhibited compensatory growth, and were not significantly different from their controls after two, two, and six weeks of *ad libitum* feeding respectively (Fig. 5A, C, and D). The Salmon

Creek treatment group housed at 20°C did not exhibit compensatory growth after *ad libitum* feeding for six weeks and remained significantly different from its control group throughout the experiment (Fig. 5B). Growth in the treatment groups housed at 20°C was inhibited, with a larger difference between control and treatment groups for all cohorts except Cowee Creek compared to stream cohort counterparts housed at 10°C (Fig. 5; Table 2).

At 10°C, all four diet treatment groups exhibited compensatory growth. Food-deprived groups had significantly lower PWC than their respective controls after two weeks of starvation. Auke Creek, Salmon Creek, Cowee Creek and Mendenhall River treatment groups all exhibited compensatory growth and were not significantly different from their respective controls after four, two, four, and two weeks of *ad libitum* feeding respectively (Fig. 5 E-H; Table 2).

Discussion

Coastrange Sculpin exhibited compensatory growth when fed salmon eggs after enduring a period of food deprivation. I predicted that treatment fish would exhibit compensatory growth during eight and six weeks of *ad libitum* feeding in the field under natural conditions and in the laboratory at a moderate temperature of 10°C, respectively, but that compensatory growth would be prevented at a relatively high temperature of 20°C in the laboratory. In the field experiment the treatment groups at all three sites exhibited compensatory growth, supporting my predictions. However, the time period required to catch up with their respective controls varied from two to six weeks. In the laboratory all four treatment groups exhibited compensatory growth at 10°C, supporting my predictions. At 20°C compensatory growth was observed in three out of four treatment groups by the end of the experiment contrary to my predictions, but growth was suppressed compared to counterparts housed at 10°C. Only the Salmon Creek treatment group did not exhibit compensatory growth at 20°C. Temperature influenced growth rates in Coastrange Sculpin and mediated the ability of sculpin to undergo compensatory growth. Stream of origin also affected growth of sculpin in both the field and laboratory and interacted with the mediating effects of temperature on the compensatory growth response.

In the field, the Auke Creek cohort exhibited the greatest percent change in weight during the experiment, with Salmon Creek and Cowee Creek cohorts having the middle and lowest PWC values respectively. Higher temperature allows for greater digestion and assimilation rates in fishes (Brett 1971, Armstrong and Schindler 2013). Adult Slimy Sculpin in an Alaskan Arctic

lake digested food nearly twice as quickly at typical summer temperatures (8-16°C) compared to winter temperatures (4°C; Hershey and McDonald 1985). The average mid-summer temperatures at Auke, Salmon, and Cowee creeks are approximately 16°C, 10°C, and 7°C respectively. The differences in summer stream temperatures may have led to the observed pattern of cohort PWC with the highest overall growth at the warmest temperatures. The Auke Creek treatment group took the longest period of time to catch up with their control group. Salmon Creek and Cowee Creek treatment groups had the middle and shortest periods of time, respectively, to catch up with their control groups. Higher temperatures leading to elevated basal metabolism (Clarke and Johnston 1999) may have increased weight loss in food-deprived fish while allowing for greater overall growth of control fish. This would lead to food-deprived fish having an even greater growth deficit to overcome and a longer catch up period. The effects of temperature on growth rate and metabolism for both food-deprived and control fish might have resulted in the extended catch up period for the Auke Creek treatment group and sequentially shorter catch up periods for Salmon Creek and Cowee Creek treatment groups.

In the laboratory where temperature was controlled, increased temperature exaggerated the separation of treatment fish PWC from their respective controls and lengthened the time needed to catch up through compensatory growth. Throughout the experiment the difference between control and treatment group PWC values were greater for cohorts housed at 20°C compared to their stream site counterparts housed at 10°C (Fig. 5). The food deprivation period resulted in a lower PWC value at week 2 for diet treatment groups housed at 20°C compared to their 10°C stream site counterparts for all four stream cohorts, demonstrating the effects of increased temperature on elevated basal metabolism. The Salmon Creek cohort showed this most drastically, being unable to exhibit compensatory growth when housed at 20°C, but catching up with their respective control group after only two weeks of feeding at 10°C. The Mendenhall cohort took six weeks to catch up with their controls when housed at 20°C, but like Salmon Creek caught up with their respective control group after only two weeks of *ad libitum* feeding at 10°C. Both of these streams are relatively cold, so the negative effects of increased temperatures may have been greater on treatment groups from these sites resulting in inhibited or prolonged compensatory growth.

In the 10°C treatment tank all four treatment groups exhibited compensatory growth within the six-week *ad libitum* feeding period. In a temperature tolerance study using Slimy Sculpin 10°C was identified as the final thermal preferendum temperature (Otto and Rice 1977). Perhaps 10°C is near an optimal metabolic thermoregulatory temperature for Coastrange Sculpin as well, reducing basal metabolic demands while maintaining digestive potential.

The benefits of compensatory growth can include improved feeding opportunities, higher dominance status, reduced risk of predation, increased reproductive success and other size related factors (Ali et al. 2003). However, in some cases compensatory growth and/or the associated growth depression leading to compensatory growth can have immediate or delayed costs. Behavioral changes in the feeding strategy of fish undergoing compensatory growth can lead to increased vulnerability to predation (Damsgård and Dill 1998, Lankford et al. 2001). Another source of mortality can come from a higher rate of winter mortality despite full compensation in size, as observed in wild reared brown trout exposed to varying periods of food deprivation (Johnsson and Bohlin 2006). There are also developmental costs associated with accelerated growth. Pumpkinseed Sunfish *Lepomis gibbosus* with a faster somatic growth rate had delayed cranial bone ossification (Arendt and Wilson 2000), weaker scales, and compromised skeletal development (Arendt et al. 2001). Other species have exhibited reduced swimming endurance after accelerated growth, which was might have negative impacts on reproductive success (Billerbeck et al. 2001, Royle et al. 2006). Many of these costs of compensatory growth are associated with juvenile fish development. The Coastrange Sculpin used in this study were beyond the early developmental stages where many of these costs present themselves, but the long term effects of compensatory growth on Coastrange Sculpin remain unexplored.

The compensatory growth response is not an all-or-nothing physiological response to food deprivation. I observed variability in compensatory growth rates between populations from unique streams, and between individuals within streams. Life stage, body size, competitive aggression, environmental conditions, and other characteristics of individual fish might influence the magnitude of the compensatory growth response among individuals in a population. The compensatory growth response may also be genetically mediated when optimal size or growth rates differ for life history stages of distinct fish populations (Fraser et al. 2007).

Based on my results, I might expect Coastrange Sculpin to exhibit compensatory growth more frequently if trends of warming and reduced duration of salmon spawning continue. Warmer rain-fed stream Coastrange Sculpin populations will likely have high growth rates when salmon eggs are abundant, but will experience greater weight loss during periods of low food availability. Populations of Coastrange Sculpin in glacier-fed streams might exhibit compensatory growth less frequently because lower temperatures reduce the metabolic impacts of limited food availability. As warming continues and glacial influence diminishes in these streams, sculpin may be able to exploit thermal heterogeneity to increase their rates of digestion during salmon spawning and maintain a low basal metabolism during periods of low food availability. Coastrange Sculpin used in the field study were confined to their enclosures and unable to exploit thermal heterogeneity within the stream, which could allow for metabolic regulation during periods of food absence and abundance in wild populations.

Compensatory growth might become a more physiologically important process for Coastrange Sculpin if projected temperature increases and climate variability in Southeast Alaska continue (Shanley et al. 2015). Coastrange Sculpin inhabit a wide geographic area from California to the Aleutian Islands, and as a species are adapted to a wide range of hydrological conditions and water temperatures. Global climate change has brought major changes to Southeast Alaska, particularly in the discharge, nutrient load, and temperature regime patterns of freshwater streams (Hood and Berner 2009). During winter, warmer temperatures are reducing winter snowpack (Stewart 2009), which reduces summer stream flow and warms water temperatures. Warming is already causing some rain-fed streams in Southeast Alaska like Auke Creek to experience extremely high temperatures during the summer. Glacier-fed systems will experience changes in temperature and flow regimes as glacial coverage continues to diminish and rain contributes more to annual discharge. However, the moderate warming of heavily glacier-fed streams may benefit sculpin through improved digestive and assimilation capacities. There may be benefits for salmon populations as well in terms of thermal stability with future reductions in glacier-fed streams (Fellman et al. 2014), which in turn would benefit sculpin that rely heavily on these salmon subsidies. My findings demonstrate that Coastrange Sculpin are capable of exhibiting compensatory growth when provided abundant salmon eggs after a period of food deprivation and that elevated temperatures can increase overall growth given sufficiently available food, but can suppress or completely inhibit compensatory growth.

Chapter 1 Figures

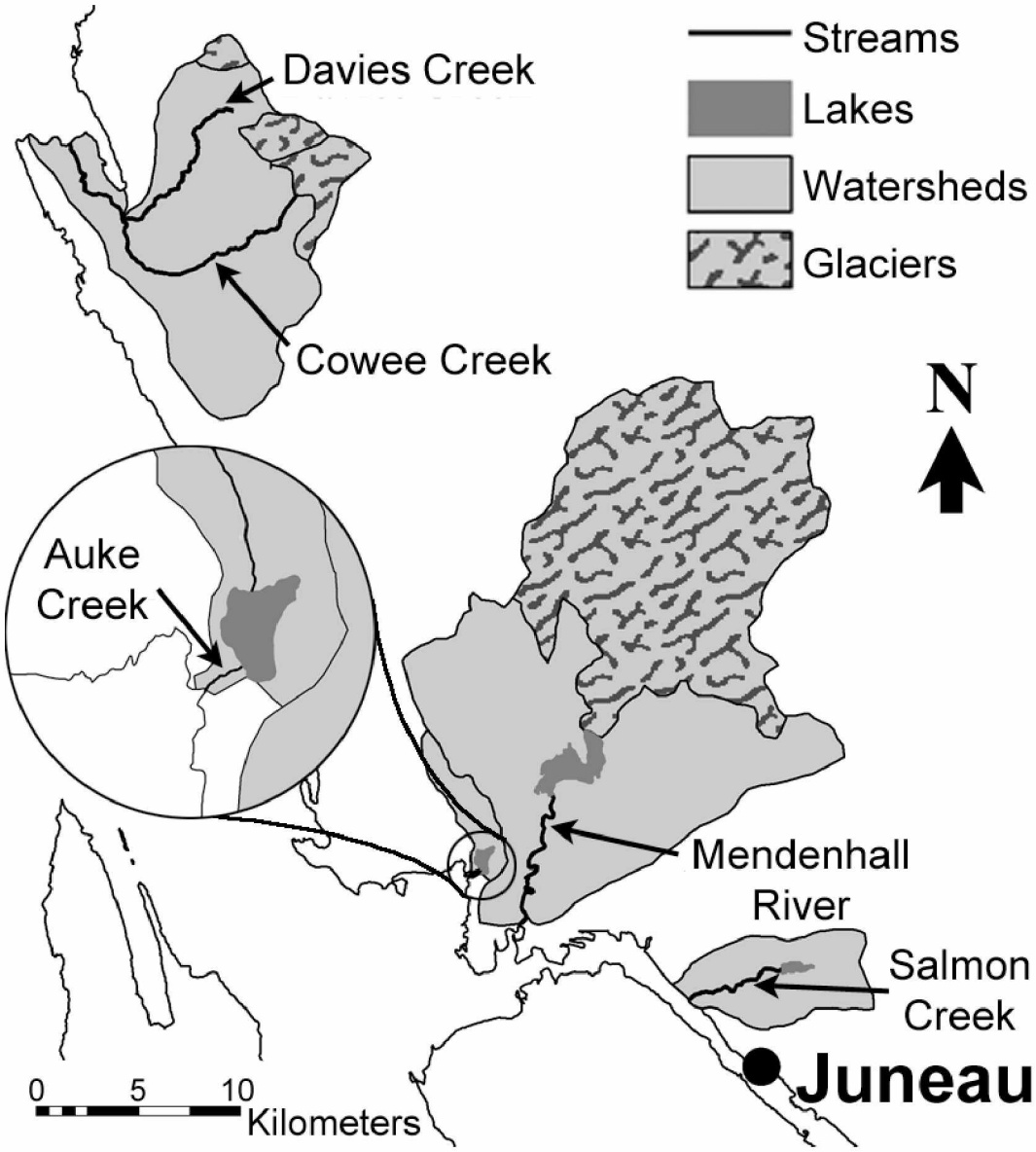

Figure 1.—Map of the study area including the four Juneau area streams where Coastrange Sculpin were collected and the corresponding stream watershed areas with glacial coverage.

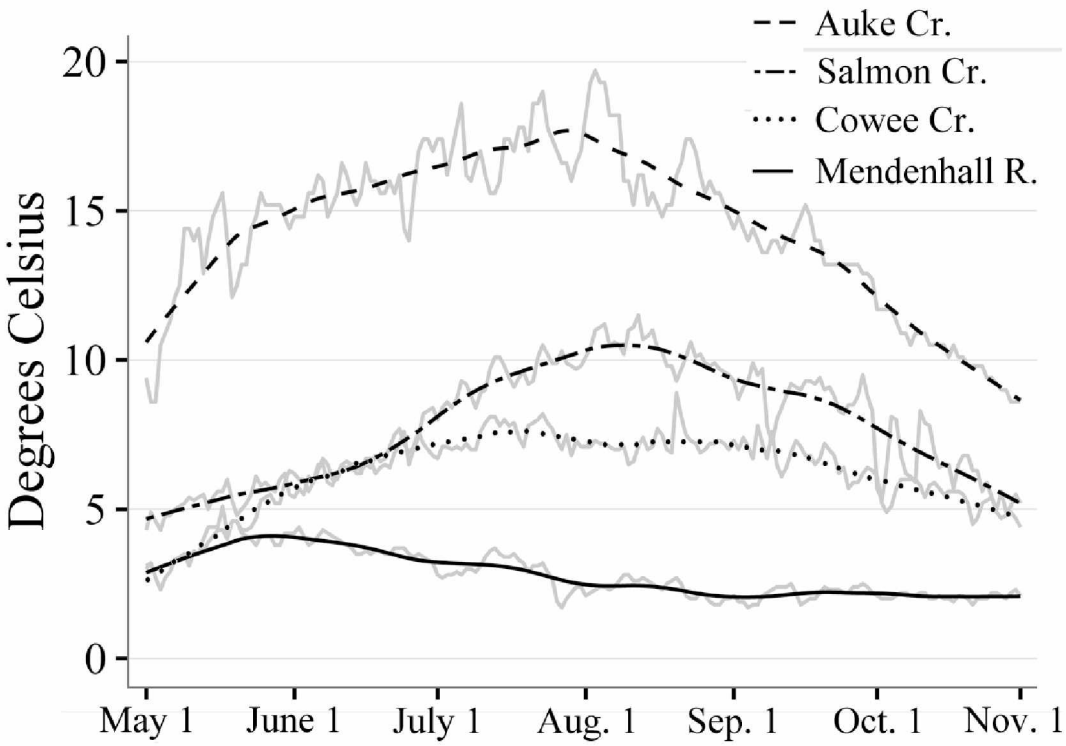

Figure 2.—Temperature regime patterns for Auke Creek (2014), Salmon Creek (2014), Cowee Creek (2011), and the Mendenhall River (2011) from May through October. Solid gray lines represent daily temperature data underlying the smoothed curves for each stream system. Supporting data was granted by Fellman et al. (2014; Cowee Cr. and Mendenhall R.), the Auke Creek weir (Auke Cr.), and the U.S. Geological Survey (Salmon Cr.). (Figure adapted from Fellman et al. 2014.)

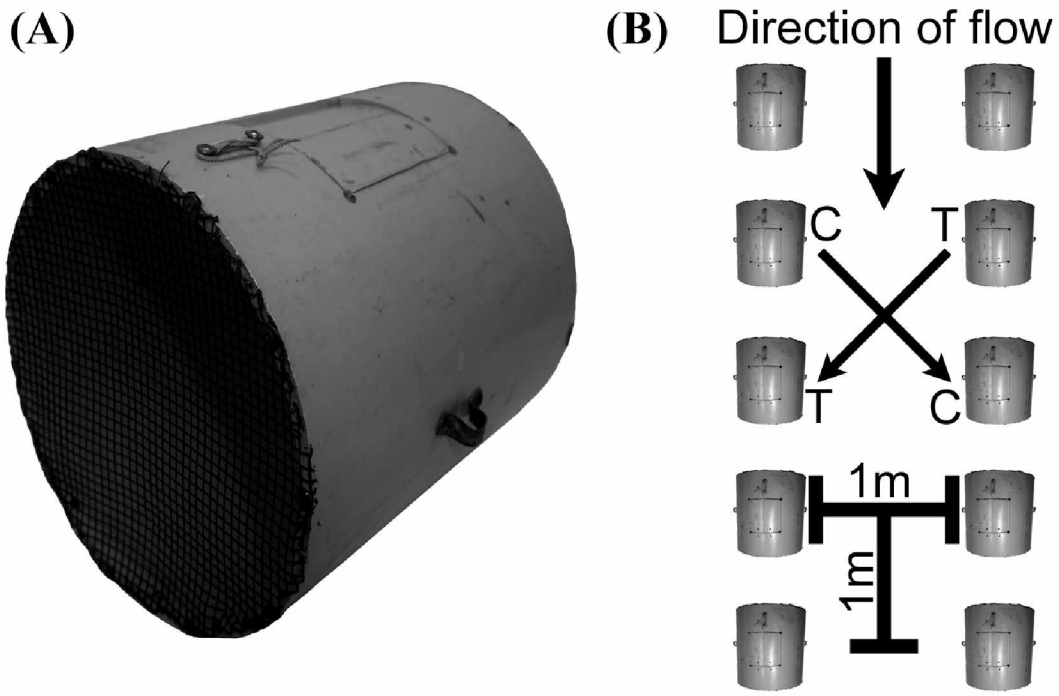

Figure 3.— **(A)** A PVC pipe enclosure with wire mesh coverings used in the field experiment and **(B)** the placement of the enclosures in the field showing direction of stream flow, the alternating pattern of control "C" and treatment "T", and the distance between enclosures.

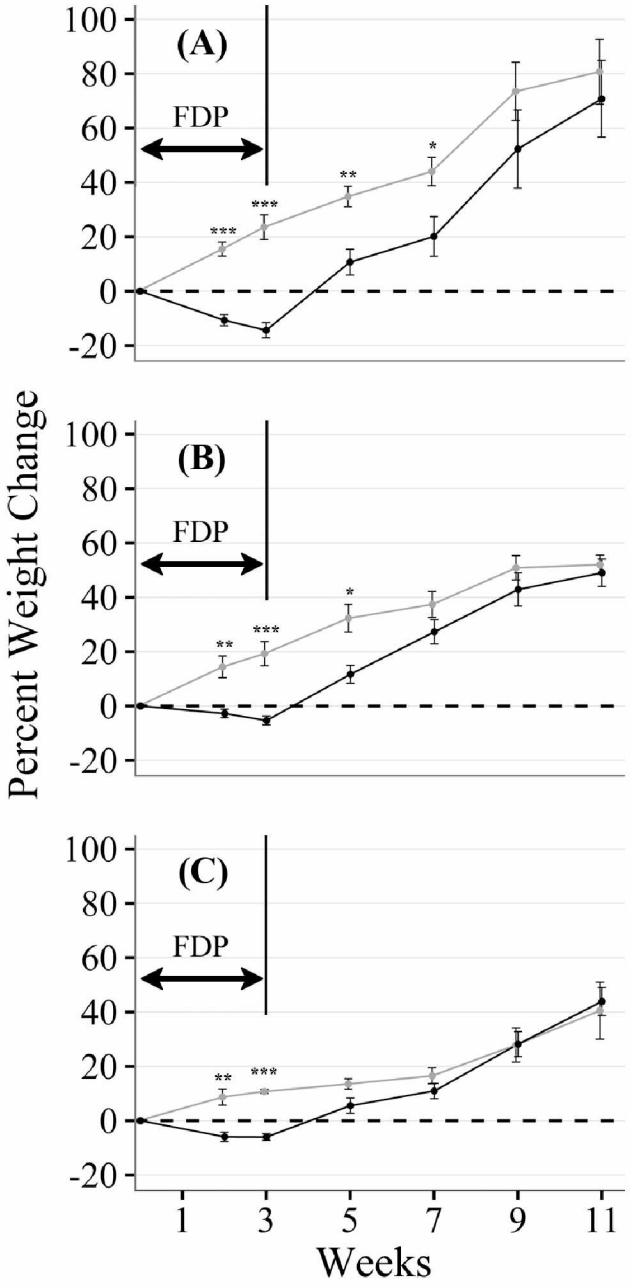

Figure 4.—Percent weight change over time for field experiment stream sites **(A)** Auke Creek, **(B)** Salmon Creek, and **(C)** Cowee Creek. Solid black lines represent the treatment groups and solid grey lines represent control groups at each stream site. Points at each sample week are the mean (n=5) with standard error bars. The first three weeks of the experiment were the food deprivation period (FDP) for the treatment group. Significance levels are: $P \leq 0.10$ •, $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***.

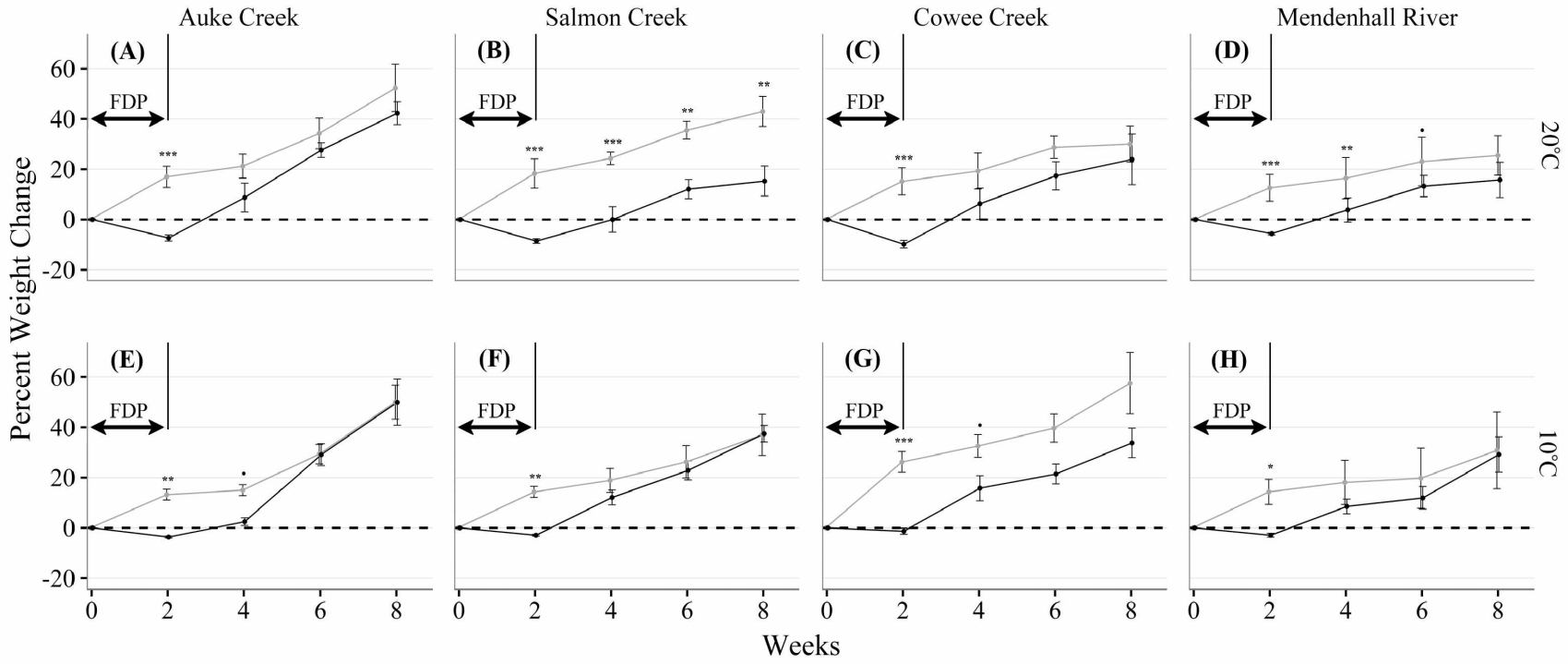

Figure 5.—Percent weight change over time for laboratory experiment stream sites in the 20°C treatment tank: **(A)** Auke Creek, **(B)** Salmon Creek, **(C)** Cowee Creek, and **(D)** Mendenhall River; and the 10°C treatment tank: **(E)** Auke Creek, **(F)** Salmon Creek, **(G)** Cowee Creek, **(H)** and Mendenhall River. Solid black lines represent the treatment groups and solid grey lines represent control groups at each stream site. Points at each sample week are the mean (n=5) with standard error bars. Control groups from Mendenhall River 20°C and 10°C, and Cowee Creek treatment group had a single individual removed (n=4). The first two weeks of the experiment were the food deprivation period (FDP) for the treatment group. Significance levels are: $P \leq 0.10$ •, $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***.

Chapter 1 Tables

Table 1.—The ANOVA test statistics for the field experiment three-way ANOVA and the laboratory experiment four-way ANOVA with response variables of percent weight change in both ANOVAs. Includes F-values, degrees of freedom, and *P*-values for all factors included in each ANOVA. Values considered significant at $\alpha < 0.05$.

	Factors	F-value	DF1,2	*P*-value
Field	Diet	138.9	1, 154	<0.001
	Stream	20.3	2, 154	<0.001
	Time	117.7	5, 154	<0.001
	Diet:Stream	11.8	2, 154	<0.001
	Diet:Time	16.3	5, 154	<0.001
	Stream:Time	3.1	10, 154	0.001
Lab	Diet	169.2	1, 253	<0.001
	Stream	6.2	3, 253	<0.001
	Time	125.7	3, 253	<0.001
	Temperature	8.4	1, 253	<0.001
	Diet:Stream	1.1	3, 253	0.367
	Diet:Time	17.0	3, 253	<0.001
	Diet:Temperature	9.1	1, 253	0.003
	Stream:Time	2.4	9, 253	0.013
	Stream:Temperature	3.6	3, 253	0.013
	Time:Temperature	1.6	3, 253	0.186
	Diet:Stream:Time	0.5	9, 253	0.900
	Diet:Stream:Temperature	6.0	3, 253	<0.001
	Diet:Time:Temperature	0.1	3, 253	0.981
	Stream:Time:Temperature	0.4	9, 253	0.916

Table 2.—The t-test P-values comparing percent weight change of diet treatment groups from the four study streams with their respective controls at discrete sample weeks for both field and laboratory experiments. Includes the difference in mean percent weight change between controls "C" and treatments "T" at each sample week (ΔC-T). Reported P-values have been adjusted for multiple comparisons with the Bonferroni method and values are considered significant at $\alpha < 0.05$.

	Sample Week	Auke Creek		Salmon Creek		Cowee Creek		Mendenhall River	
		ΔC-T	P-Value	ΔC-T	P-Value	ΔC-T	P-Value	ΔC-T	P-Value
Field	2	26.2	<0.001	17.2	0.002	14.6	0.003	-	-
	3	37.9	<0.001	24.6	<0.001	16.8	<0.001	-	-
	5	24.1	0.002	20.6	0.015	8.0	0.621	-	-
	7	23.9	0.010	10.1	1.0	5.6	1.0	-	-
	9	21.2	0.261	7.9	1.0	-0.3	1.0	-	-
	11	10.0	1.0	3.0	1.0	-3.4	1.0	-	-
Lab 20°C	2	24.3	<0.001	26.8	<0.001	25.0	<0.001	18.2	<0.001
	4	12.5	0.13	24.3	<0.001	13.0	1.0	12.6	0.008
	6	6.6	1.0	23.4	0.006	11.3	1.0	9.8	0.052
	8	10.0	1.0	27.7	0.002	6.1	1.0	9.7	0.110
Lab 10°C	2	16.9	0.002	17.2	0.002	27.5	<0.001	17.3	0.011
	4	12.6	0.078	6.8	1.0	16.8	0.082	9.6	1.0
	6	0.2	1.0	3.4	1.0	18.2	0.143	7.8	1.0
	8	0.1	1.0	-0.4	1.0	23.8	0.204	1.6	1.0

Supplementary Table S1.—Starting weights, measured in grams, of Coastrange Sculpin used in the analysis of both field and laboratory studies from Auke, Salmon, and Cowee creeks as well as Mendenhall River.

Individual		Individual fish weight (g)			
		Auke Creek	Salmon Creek	Cowee Creek	Mendenhall River
Field					
Treatment	1	10.23	19.10	11.87	-
	2	9.85	14.82	11.98	-
	3	8.69	17.48	13.46	-
	4	16.56	18.99	11.93	-
	5	15.85	16.75	20.80	-
Control					
	1	13.37	11.81	14.00	-
	2	18.70	15.89	11.99	-
	3	7.35	16.30	15.00	-
	4	26.44	15.90	18.41	-
	5	8.60	14.34	11.27	-
Lab 20°C					
Treatment	1	19.98	10.08	6.31	8.35
	2	18.00	9.92	6.75	16.16
	3	15.57	8.77	8.60	11.61
	4	11.36	14.34	8.10	11.65
	5	13.36	18.66	4.54	9.56
Control					
	1	10.98	11.16	9.34	8.20
	2	12.41	18.31	3.34	8.06
	3	10.81	12.14	4.86	9.93
	4	11.38	7.70	5.26	13.35
	5	7.47	14.86	4.50	9.05
Lab 10°C					
Treatment	1	13.33	8.37	6.21	8.31
	2	18.09	12.95	18.17	16.43
	3	17.42	13.95	8.63	20.98
	4	23.86	12.14	6.95	13.50
	5	7.61	13.19	5.24	19.69
Control					
	1	12.91	18.39	12.53	13.08
	2	9.80	32.02	6.56	6.64
	3	7.80	15.45	5.03	8.71
	4	18.42	15.35	4.28	14.96
	5	16.10	13.60	8.50	10.46

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Appendix

(907) 474-7800

(907) 474-5993 fax uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 21, 2015

To: David Tallmon, PhD
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [462612-8] The importance of marine derived nutrients to coastrange sculpin fitness.

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	July 10, 2015
Initial Approval Date:	July 8, 2013
Effective Date:	July 21, 2015
Expiration Date:	July 8, 2016

This action is included on the July 23, 2015 IACUC Agenda.

PI responsibilities:

- Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.
- Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)
- Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.
- Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.
- Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".

Chapter 2: The Effect of Spatial and Temporal Prey Availability on the Use of Habitat by Brown Bears *Ursus arctos* in Berners Bay, Southeast Alaska.

Abstract

Pacific salmon *Oncorhynchus* spp. bring food and nutrients from the marine environment into freshwater ecosystems. In many regions, coastal brown bears *Ursus arctos* rely heavily on the pulsed subsidy of salmon as a food source and spread marine-derived nutrients deep into the riparian zone. Not all bears use the salmon resource equally however. Sex, age, and reproductive status can affect dominance behavior and access to salmon at bear fishing location, but this varies regionally and between populations. I examined the spatial and temporal distribution of brown bears in Berners Bay, Southeast Alaska. The objective of this study was to characterize how bears shift their distribution in response to salmon availability. Further, I examined whether reproductive status, identified by the presence of cubs, affected use of habitat near salmon spawning reaches in adult females. I found that adult females without cubs and adult males used space within 100 m of spawning reaches 8-13% more than juveniles and adult females with cubs. Based on their use of space when salmon were available, adult females without cubs were identified as dominant along with adult males. Adult females with cubs used space similarly to juvenile groups and were identified as subdominant. The behavioral differences between adult females based on reproductive status may be related to the increased risk of infanticide by adult males for females accompanied by cubs. Increased human disturbance to Berners Bay via construction of a proposed road might decrease the number of salmon fishing locations available for brown bears, potentially increasing competition and affecting social interactions at remote fishing locations.

Introduction

Pacific salmon *Oncorhynchus* spp. are a pulsed subsidy that bring marine nutrients from the open ocean to coastal ecosystems and impact these inland ecosystems in a variety of ways. Salmon-derived nutrients increase productivity of biofilm and macroinvertebrates in freshwater streams (Wipfli et al. 1998, 1999), which in turn benefit resident fishes (Wipfli et al. 2003). Stream fish that consume salmon eggs and flesh have higher growth rates and increased body

[2]Godin, M. and D. Tallmon. 2017 The effect of spatial and temporal prey availability on the use of habitat by brown bears Ursus arctos in Berners Bay, Southeast Alaska. Formatted for submission to Transactions of the American Fisheries Society.

condition (Bilby et al. 1996, Foote and Brown 1998, Heintz et al. 2004, Rinella et al. 2012, Swain et al. 2014).

The spread of salmon-derived nutrients away from the stream is facilitated by a host of riparian predators, but in many areas brown bears *Ursus arctos* play a major role (Helfield and Naiman 2006). Brown bears distribute 99% of the nitrogen they ingest from consuming salmon into the riparian zone through their urine and feces (Hilderbrand et al. 1999a). Carcass remnants left by bears further spread nutrients into the riparian zone (Ben-David et al. 1998, Gende et al. 2004), and increase opportunities for other scavengers to benefit from the pulsed salmon resource (Winder et al. 2005, Hocking and Reimchen 2006). Elevated levels of $\delta^{15}N$ isotopes indicative of marine-derived nutrients are measurable in plant growth out to 500 m from salmon streams, well beyond the functional distance of soil leeching and flooding (Ben-David et al. 1998, Hilderbrand et al. 1999a). Without bears transporting as much as 50% of the available salmon nutrients from the stream into the riparian zone, the majority of carcasses would rapidly be washed downstream and their nutrients lost from the local ecosystem (Ruggerone et al. 2000, Gende et al. 2004, Quinn et al. 2009).

Salmon have profound influences on coastal brown bear abundances, distributions, and social interactions. Brown bear populations with reliable access to salmon can have densities 55 times greater than inland populations that are primarily vegetarian (Hilderbrand et al. 1999b), though many other geographic and environmental differences influence population densities. In areas where salmon availability is restricted both spatially and temporally as a result of thermal heterogeneity at spawning locations, with unique salmon runs being available for only a few weeks at different streams, brown bears cover great distances to track the abundance of salmon across the landscape (Schindler et al. 2013). In years where salmon abundance is high, brown bears show an increased likelihood of taking salmon away from the stream to feed (Quinn et al. 2009). Subdominant sex-age groups are more likely to retreat into the riparian zone after capturing salmon to avoid confrontation with dominant bears (Gende and Quinn 2004). Subdominant bears avoid high concentrations of bears, such as at prime fishing locations (Nevin and Gilbert 2005a, Suring et al. 2006). Subsequently, subdominant bears use sub-prime fishing locations more often in an effort to avoid conflict with dominant bears (Egbert and Stokes 1976, Ben-David et al. 2004, Gende and Quinn 2004). At these sub-prime locations subdominant bears sometimes develop unique fishing strategies and can be as successful as dominant bears fishing

at prime locations (Gill and Helfield 2012). In some cases subdominant bears use salmon to a far lesser degree. On Admiralty Island near Juneau, Alaska, a segment of the brown bear population consisting mostly of females remains in upper-elevation habitats year round and does not use salmon as a food source despite close proximity to salmon streams (Schoen et al. 1986).

Large adult male brown bears have higher metabolic requirements compared to smaller females and juveniles and are limited to calorie dense foods that can be rapidly consumed (Welch et al. 1997, Rode et al. 2001). The high metabolic cost associated with this large size makes adult males more dependent on easily accessible and highly nutritious food sources like salmon to put on fat stores for winter (Hilderbrand et al. 1999b, Rode et al. 2006). When bears congregate at salmon fishing locations the large adult male brown bears are most often dominant and smaller juvenile bears are often subdominant (Egbert and Stokes 1976, Gende and Quinn 2004, Nevin and Gilbert 2005a, Gill and Helfield 2012, VanDaele et al. 2013). Differences in body size and the corresponding differences in metabolic costs likely drive the observed dominance hierarchy at salmon fishing locations.

Adult females are generally smaller in size than adult males and often act as subdominant when fishing for salmon. However, the collective metabolic demands of adult females with growing cubs are much higher than those of juveniles or females without cubs. Females with cubs have to procure food for themselves and their cubs during summer, as well as producing milk for the cubs in the winter den. The cost of producing milk often leads to females with cubs being in relatively poor condition upon exit from the den in spring (Hilderbrand et al. 2000). Females not able to meet their own metabolic demands during summer due to low food availability or high intraspecific competition may neglect and even abandon their cubs in order to survive (Gende and Quinn 2004). Female brown bears that use salmon as a food source can attain a larger body size and have larger litters compared to females that do not use salmon (Hilderbrand et al. 1999b). Adult females often act as subdominants in order to avoid conflict (Stonorov and Stokes 1972, Egbert and Stokes 1976, Nevin and Gilbert 2005a, 2005b, Gill and Helfield 2012) or infanticide by adult males (Ben-David et al. 2004, Bellemain et al. 2006). However, in certain circumstances female bears have been observed displaying aggressive dominant behavior to secure prime fishing locations even when accompanied by cubs (Stonorov and Stokes 1972, Egbert and Stokes 1976, Gende and Quinn 2004).

This study focuses on brown bears in Berners Bay near Juneau, Alaska. The objective of this study were to determine: 1) whether brown bears use salmon spawning streams differently when salmon are available compared to when salmon are not available 2) whether brown bears use salmon spawning streams differently depending on their sex and age 3) whether adult female brown bears act as dominant or subdominants, and whether reproductive status affects this dominance. A motivating factor for the analysis of brown bears in this area is a proposed road that would extend the Juneau road system through Berners Bay, potentially disturbing habitat connectivity and increasing human access to the area.

I predicted that brown bears would use space in proportion to its availability around salmon spawning streams when salmon are not present and disproportionately more when salmon are spawning. Assuming adult males to be dominant as a group and juveniles to be subdominant, I evaluated the hypothesis that adult female bears would act as subdominants and use habitat within 100 m of salmon spawning streams significantly less than dominant adult male bears. Further, I predicted that female brown bears would act as subdominants irrespective of their reproductive status, identified by the presence of cubs.

Methods

I used brown bear GPS telemetry data collected from 2006 through 2011 by Flynn et al. (2012) in Berners Bay near Juneau, Alaska (Fig. 1). Berners Bay has four major drainage valleys: Berners River, Lace River, Cowee Creek, and the Antler-Gilkey drainage. There are over a dozen stream systems resulting in over 200 km of major stream length in the Berners Bay watershed. Salmon are available from July through October and are vulnerable to predation by brown bears over more than 25 km of stream length throughout Berners Bay. The brown bear telemetry data were collected as part of a study evaluating wildlife crossing locations for the proposed Juneau Access Improvements Project road corridor, which would run 78 km along the coast of Lynn Canal through Berners Bay. Brown bears were captured in the Berners Bay estuary using foot snares set along travel corridors and by darting animals from a helicopter. Bears captured in snares and those shot from the air were immobilized using Telazonl ® darts (Fort Dodge Animal Health, Fort Dodge, Iowa, USA). Tooth and hair samples were collected to determine sex and age. Brown bears were then fitted with GPS collars (Telonics Inc., Models TGW-3600, 3700, 3790, Mesa, AZ), which were set to collect location fixes every 20 or 30 minutes from spring through November. The collars were set to release after 10-16 months at

which point they were retrieved using a Very High Frequency transmitter. The data were downloaded and converted to a GIS database (ArcGIS 10, ESRI, Redlands, CA).

The analysis for my study consisted of spatially and temporally subsampling the telemetry data (Flynn et al. 2012), using ArcGIS. A relatively small number of location fixes for brown bears that traveled outside of the study area were removed for the purposes of my study, which focused only on the Berners Bay drainage basin (Fig. 1). Brown bears have access to over a dozen stream systems that host runs of Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, Sockeye Salmon *O. nerka*, and Coho Salmon *O. kisutch* in Berners Bay. Using aerial salmon survey data from the Alaska Department of Fish and Game, the bear telemetry data were divided into two equal seasons of salmon availability. This salmon survey data consisted of aerial surveys conducted every 2-4 weeks from July through October for the Berners Bay marine and freshwater systems. The period where salmon were not present in rivers entering Berners Bay, "non-salmon season" here forward, was designated as the period from May 1st through June 30th. The period where salmon were present in Berners Bay, "salmon season" here forward, was designated as the period from July 15th through September 15th. The period between the two seasons from July 1st through July 14th was omitted to account for interannual variation in the onset of salmon runs in Berners Bay.

Sites in Berners Bay where spawning salmon were vulnerable to predation by brown bears were identified by Flynn et al. (2012) prior to collecting brown bear location data for their study. Salmon were vulnerable to predation in these reaches due to shallow depth, or other stream characteristics. These sites will here forward be referred to as spawning reaches (Fig. 1). Distance from spawning reach categories (DSCs) of 0-100, 101-250, 251-500, and 501-1000 m from each spawning reach were constructed using ArcGIS (Fig. 1).

For each individual brown bear, the telemetry data were subsampled to include only a single random location fix for each unique calendar day. This had several benefits for the following analysis. The location fix rate was not uniform among all bear collars due to individual settings and missed location fixes, so random subsampling of the data equalized the location fix rate across individuals. By extending the duration between individual relocations, bears were allowed sufficient time to traverse the largest 1000 meter DSC surrounding each of the spawning reaches (McLellan and Shackleton 1988). Systematic subsampling of the data alleviates some of the effects of autocorrelation (McNay et al. 1994), though autocorrelation is inherent in all

wildlife telemetry data even with weeks between relocations (Rooney et al. 1998, Otis and White 1999, Cushman et al. 2005). A study on autocorrelated movements of brown bears found that individuals had highly autocorrelated movements up to, but not after, 24 hours between relocations (Boyce et al. 2010), further supporting a random daily subsample.

The individual data were grouped into five sex-age groups based on sex, age, and reproductive status. The location data from 34 individual bears were used consisting of 10 adult males, 8 juvenile males, 4 juvenile females, 5 adult females without cubs, and 7 adult females with cubs. Juvenile brown bears were defined as individuals aged five years or younger. Adults were defined as individuals older than five years of age (Egbert and Stokes 1976). Finally, the data for each group were overlaid on the spawning reach DSCs, and the number of location fixes in each of the four DSCs was recorded.

The area of each DSC was calculated using ArcGIS and the relative percent area for each DSC was calculated as 5.6, 10.5, 22.5, and 61.4 percent for 0-100, 101-250, 251-500, and 501-1000 meter DSCs respectively. If brown bears used these DSCs in proportion to their availability, then the observed counts in each DSC will not be significantly different from the expected values calculated using the DSC areas.

The subsampled data were analyzed using the G-test method described by Sokal and Rohlf (1995) and used by McLellan and Shackleton (1988). A G-test analysis was conducted on both the non-salmon season and salmon season data sets independently. To determine if the combined groups used space around spawning reaches in proportion to its availability, the data for all five groups was pooled and observed values were compared to expected values (G_P). To determine if use of space was dissimilar among groups, all five groups were analyzed against each other to test for heterogeneity (G_H; Sokal and Rohlf 1995). For all G tests, values were considered significant at $\alpha < 0.05$.

After identifying significant G-tests for the pooled data, Bonferroni confidence intervals were calculated at each DSC for both the non-salmon and salmon seasons to identify where observed values differed from expected values. These confidence intervals (90% simultaneous, 97.5% individual) were calculated following the method of Marcum and Loftsgaarden (1980) and were used to assess statistical significance. If the confidence interval did not contain the expected value, then the observed pooled values were considered to have deviated significantly from expected values under the null hypothesis.

After identifying significant heterogeneity using G-tests, significant differences between groups at each DSC were identified using the Marascuilo procedure (Marascuilo 1966, Wagh and Razvi 2016). The Marascuilo procedure is specifically designed to compare multiple proportions after significant G or chi-squared tests. This procedure allows for the pairwise comparisons between the five sex-age groups within each DSC individually using a critical range derived from the chi-squared distribution. If the absolute difference between groups is greater than the calculated critical range, then those groups are significantly different. The critical range was calculated using the critical value of the chi-square distribution of 9.488 for a significance level of $\alpha < 0.05$ on 4 degrees of freedom.

Salmon-derived nutrients can be found as far as 500 m from salmon spawning reaches due to the spread of these nutrients by predators (Ben-David et al. 1998, Hilderbrand et al. 1999a). I assumed that observed proportions significantly greater than expected values in the 0-100, 101-250, and 251-500 meter DSCs during the salmon spawning season indicated the use of salmon as a food source. I assumed that adult males were dominant as a group and that juveniles were subdominant as a group and compared their use of space to both adult female groups to identify female dominance. The proportional use of the 0-100 meter DSC was used to determine if reproductive status affected dominance among adult female brown bears. Significant differences between adult females with and without cubs in the 0-100 meter DSC would indicate that reproductive status does affect dominance and the use of salmon as a food source by adult females.

Results

During the non-salmon season brown bears used space in proportion to its availability with the exception of the 501-1000 meter DSC, which was used slightly less than expected. During the salmon season, all the groups used the 0-100 and 101-250 meter DSCs substantially more than in proportion to their availability, demonstrating that brown bears alter their use of space to feed on salmon when available (Fig. 2). However, the sex-age groups significantly differed in their use of individual DSCs during the salmon season. Adult females without cubs used the 0-100 DSC more than any other group, and significantly more than adult females with cubs. Adult females without cubs used space similarly to dominant adult males, while those with cubs used space similarly to subdominant juveniles.

When the group data were pooled, use of space deviated from expected values during the salmon season (G_P = 3542.49, d.f. = 15, P< 0.001). The pattern of space use by brown bears was drastically different between the non-salmon and salmon seasons (Fig. 2). During the non-salmon season all five groups used the DSCs in proportion to their availability as analyzed by confidence intervals, but when the data were pooled the 501-1000 m DSC was used slightly less than expected. Conversely, during the salmon season the 0-100 and 101-250 meter DSCs were used significantly more than in proportion to their availability by all five groups individually and pooled confirming a shift in behavior to feed on salmon.

The five sex-age groups were tested for homogeneity of space use in the non-salmon and salmon seasons independently. During the non-salmon season, sex and age did not significantly affect the use of space by brown bears (G_H = 13.88, d.f. = 12, P = 0.308). During the salmon season however, significant heterogeneity existed among groups (G_H = 30.49, d.f. = 12, P = 0.002). Adult females without cubs used the 0-100 meter DSC approximately 13% more than juveniles and females with cubs. Adult males, which were classified a priori as dominant, used the 0-100 meter DSC similarly to females without cubs and approximately 8% more than juveniles and females with cubs. Adult females without cubs used the 0-100 DSC significantly more than adult females with cubs and juvenile males as analyzed with the Marascuilo procedure (Fig. 3). Juvenile females used the 0-100 DSC less than all other groups, but were not significantly different from adult females without cubs due to a smaller sample size (n=108) compared to the other groups (n= 340-731). In the 251-500 meter DSC, Adult females with cubs used space similarly to juvenile groups and approximately 8% more than adult males and females without cubs. Adult females with cubs used the 251-500 meter DSC significantly more than adult males as analyzed by the Marascuilo procedure. No significant differences among groups were observed in either the 101-250 or 501-1000 meter DSCs using the Marascuilo procedure.

Discussion

During the salmon season the combined brown bear groups used space within the 0-100 and 101-250 meter DSCs substantially more than in proportion to its availability. This is consistent with the use of salmon resources by brown bears in Berners Bay when salmon are available. All five groups used space within the 0-100 and 101-250 meter DSCs substantially more during the salmon season compared to when salmon were not available. However, space

was not used equally by different sex-age groups during the salmon season. Adult males and adult females without cubs used the 0-100 meter DSC approximately 8-13% more than adult females with cubs and juvenile groups.

I found that brown bears shifted their use of space to feed on salmon during the salmon spawning season from July 15th through September 15th. Others have found that brown bears shift their spatial distribution to track the availability of salmon across the landscape (Glenn and Miller 1980, Schindler et al. 2013, Deacy et al. 2016). In several studies of individual behavior, adult female bears were among the most dominant bears at salmon fishing locations even when accompanied by cubs (Stonorov and Stokes 1972, Egbert and Stokes 1976, Gende et al. 2004). However, adult females as a group are generally subdominant among congregations of other bears (Suring et al. 2006), and may use salmon less than other sex-age groups (Schoen et al. 1986, Ben-David et al. 2004, VanDaele et al. 2013). The findings of my study indicate that reproductive status significantly affects the use of salmon spawning reaches by adult female bears in Berners Bay.

Contrary to my initial prediction that both adult female groups would act as subdominant during the salmon season, reproductive status appears to influence the use of habitat near salmon spawning reaches by adult females. Females not accompanied by cubs used space within the four DSCs similarly to adult males, spending significantly more time in the 0-100 DSC than females with cubs. Adult females with cubs used the four DSCs similarly to subdominant male and female juvenile groups, spending more time in DSCs farther from spawning reaches (Fig. 3). Others have found that subdominant sex-age groups tend to spend less time at fishing locations and quickly retreat into the riparian zone after securing a salmon (Gende and Quinn 2004). The results of my study show a pattern of space use consistent with this type of behavior when salmon were available in Berners Bay. Subdominant juvenile and females with cubs spent less time in the 0-100 meter DSC and more time in the 251-500 meter DSC than the dominant adult males and females without cubs.

In some areas where brown bears congregate in large numbers to fish salmon that are restricted by migration barriers like waterfalls, females with cubs are dominant along with adult males. These dominant females display high levels of aggressive behavior towards all other sex-age groups (Stonorov and Stokes 1972, Egbert and Stokes 1976). This aggressive behavior is likely a method of preventing infanticide while allowing the mother and cubs access to the

limited number of prime salmon fishing locations. In Berners Bay, salmon are less spatially restricted and are vulnerable to predation along more than 25 km of stream lengths on 12 unique stream systems. This abundance of fishing locations might allow females with cubs in Berners Bay to exhibit less aggressive subdominant behavior, while still maintaining access to salmon.

The proposed Juneau Access Improvements Project (JAIP) road would run along the coast of Berners Bay and cross several rivers that host salmon runs. This road would not only incur large disturbances during construction, but would increase access to Berners Bay for hunting, fishing, and other forms of human ecotourism. Brown bears in general avoid roads, where encountering humans or vehicles is more likely (Graves et al. 2006, 2011, Martin et al. 2010). However, subdominant bears sometimes favor areas associated with roads (Graham et al. 2010), choosing the risk of human interaction over confrontation with large adult male bears. The JAIP proposed road would be constructed in close proximity to at least 6 of the 20 or so unique spawning reaches that brown bears in Berners Bay use to fish for salmon. Time spent avoiding roads and humans would decrease the amount of time bears spend fishing, and therefore total consumption of salmon during summer (Gende and Quinn 2004, Rode et al. 2006). Where prime fishing locations are frequented by humans, dominant male bears sometimes adopt a crepuscular feeding pattern to avoid humans (Olson et al. 1997, 1998). In these areas subdominant bears are allowed more fishing time without the threat of confrontation with adult males (Olson et al. 1997, 1998, Nevin and Gilbert 2005a, 2005b). Greater human access to Berners Bay with the JAIP proposed road could result in avoidance of important salmon fishing locations by brown bears. This might increase competition at more remote salmon fishing locations, potentially affecting dominance or female reproductive success.

Chapter 2 Figures

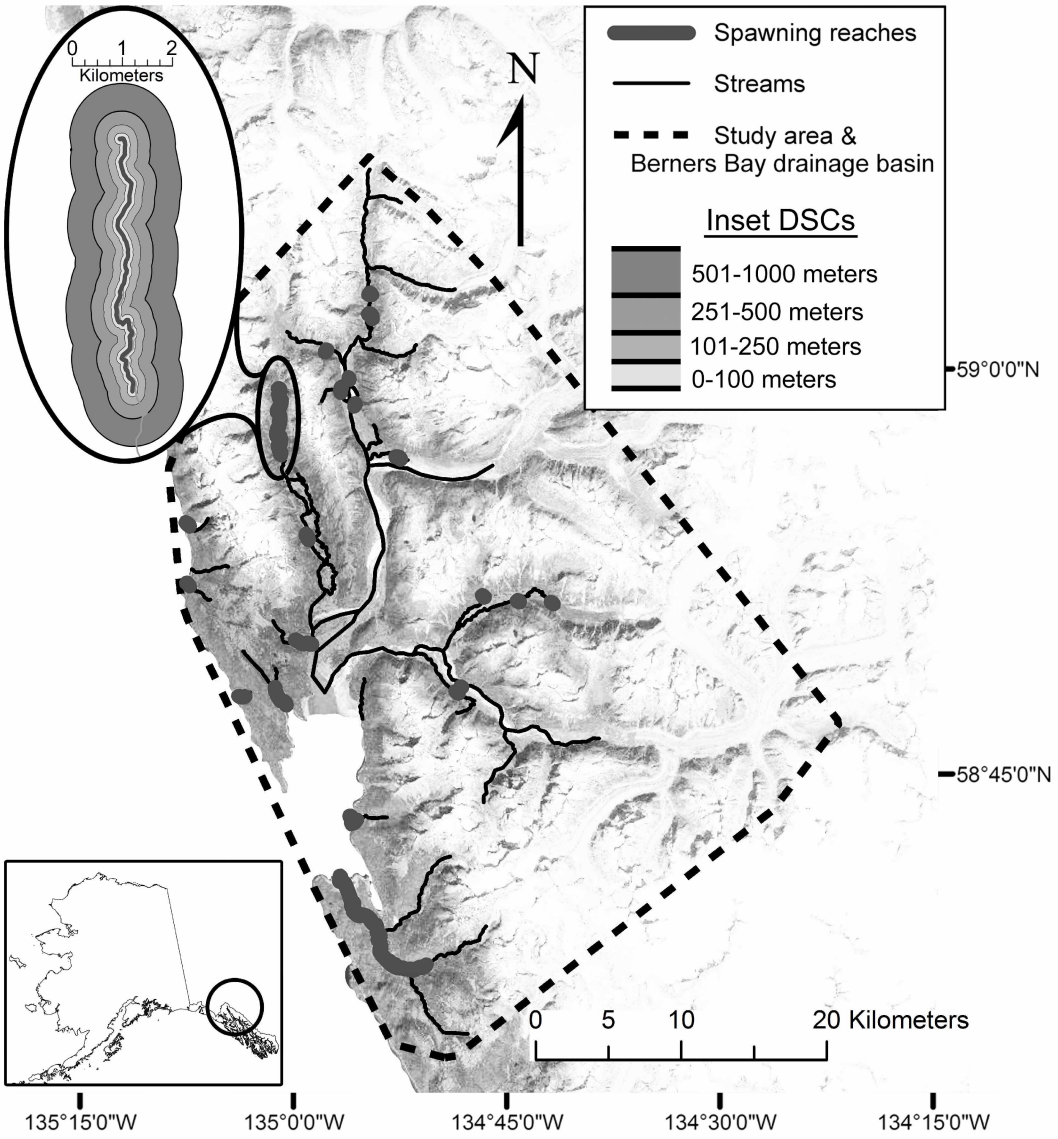

Figure 1.—Study area map of the Berners Bay drainage basin located in Southeast Alaska including the streams and salmon spawning reaches located in the drainage basin, as well as an inset example of the distance from spawning reach categories (DSCs).

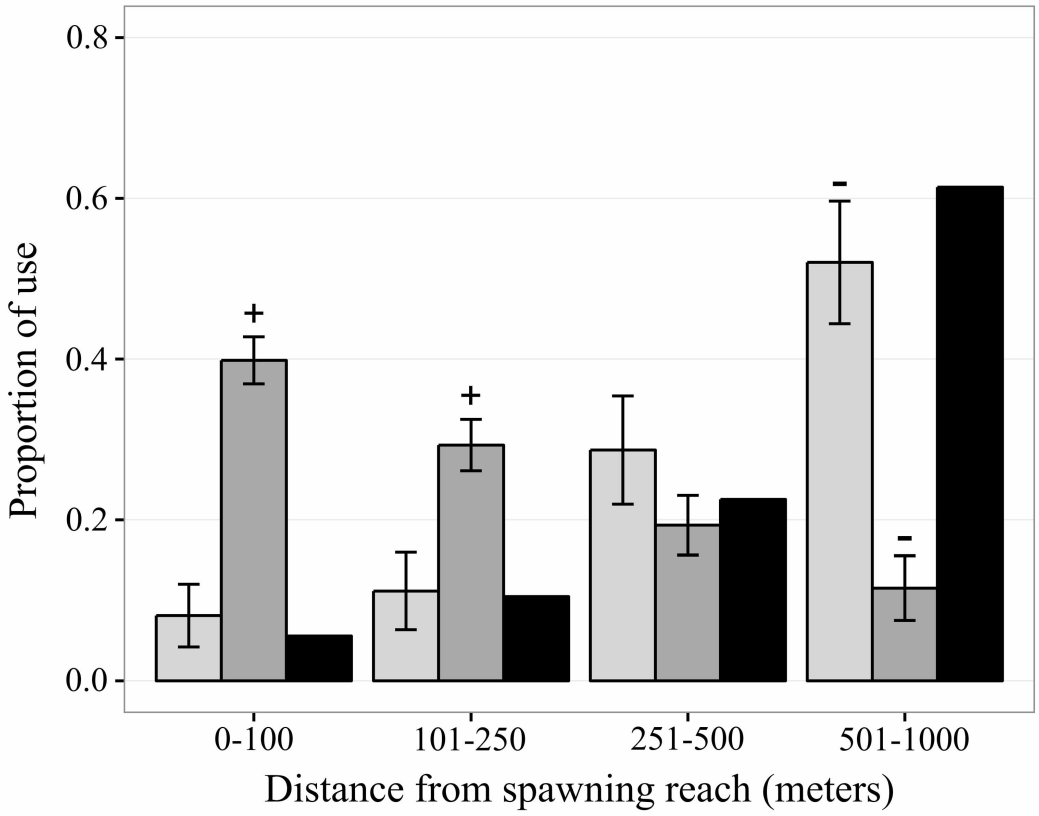

Figure 2.—Use (proportion of radio-relocations) of distance from spawning reach categories (DSCs) around salmon spawning reaches by brown bears during the: ☐ non-salmon season from 1 May through 30 June (n=394); ▩ salmon season from 15 July through 15 September (n=2038) compared to ■ expected proportions. Error bars reflect calculated confidence intervals. Significantly greater and lesser deviations of observed proportions to expected proportions, where they exist, are indicated by "+" and "-" symbols respectively.

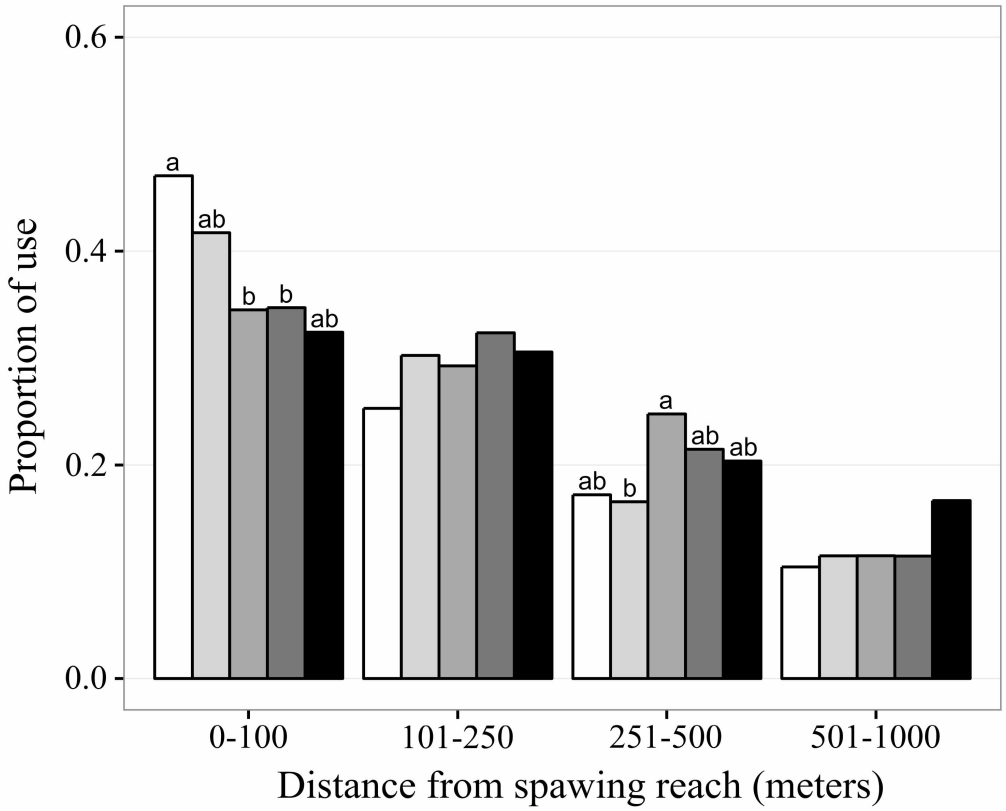

Figure 3.—Proportional use of distance from spawning reach categories (DSCs) around salmon spawning reaches during the salmon spawning season by: ☐ adult females without cubs (n=459), ☐ adult male (n=731), ☐ adult females with cubs (n=400), ☐ juvenile male (n=340), and ■ juvenile female (n=108) brown bear sex-age groups. Significant differences ($P < 0.05$) among groups use of each DSC, where they exist, are indicated by different letters.

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General Conclusion

In Southeast Alaska, habitat types change dramatically over relatively short distances. Mountain alpine and glacial icefield at higher altitude give way to conifer dominated forests which drain into ocean estuaries. A major motivation for my research was the Alaska Experimental Program to Stimulate Competitive Research or Alaska EPSCoR. This program funds projects that study the interconnected habitats and organisms in Southeast Alaska ranging from icefield to estuary. The focal organisms of my thesis use habitats along freshwater streams from headwater streams to ocean estuaries and both rely on salmon as a major food source. Pacific salmon play an important role in connecting the marine environment with freshwater and riparian habitats inland. Consumers like Coastrange Sculpin, brown bears, and a host of others congregate along salmon streams to prey on salmon during summer. Their activity serves to spread marine-derived nutrients away from the stream through carcass dispersal and excreta. The pulsed subsidy of salmon provides a highly abundant and calorie dense food source, resulting in rapid growth and behavioral changes in Coastrange Sculpin and brown bears feeding on salmon.

In Chapter 1 I demonstrated that Coastrange Sculpin are capable of exhibiting compensatory growth when being fed a temporally limited diet of salmon eggs. Sculpin housed in both field and laboratory conditions were able to undergo compensatory growth. In the field experiment, all three treatment groups exhibited compensatory growth compared to their respective control groups. However, the rate of growth and duration of the catch up period varied by stream site. Sculpin at the coldest stream grew at a slower rate overall, but were able to catch up with their control groups in the least amount of time. Alternately, Sculpin at the warmest stream grew at a much higher rate overall, but took three times as long to catch up with their control group. Other environmental, population level, and genetic factors may be influencing the trend of growth rate and catch up duration, but temperature appears to play a large role.

In the laboratory experiment, treatment fish from different stream groups were able to exhibit compensatory growth at both 10°C and 20°C. However, fewer treatment groups exhibited compensatory growth when housed at 20°C. In addition, all four treatment groups housed at 20°C exhibited greater weight loss during the starvation period and, if they did exhibit compensatory growth, they generally took a longer period to catch up to their respective control groups compared to the groups housed at 10°C.

Both field and laboratory studies confirmed that Coastrange Sculpin are capable of exhibiting compensatory growth to catch up in weight after enduring a period of food limitation. The results of the laboratory experiment and the observed trend in the field experiment indicated that while warmer temperatures allow for increased growth rates when food is available, it increases weight loss and extends the time needed for individuals to catch up after food limitation.

In Chapter 2 I demonstrated that brown bears in Berners Bay do change their use of space in relation to the availability of salmon. Brown bears used space in proportion to its availability when salmon were not available. When salmon were available, all five sex-age groups (adult males, juvenile males, juvenile females, adult females with cubs, and adult females without cubs) used space within the 0-100 and 101-250 meter DSC substantially more than in proportion to its availability. This shows that the brown bears in Berners Bay are using salmon as a food source when salmon are available.

Reproductive status, identified by the presence of cubs, affected the use of salmon by adult female brown bears in Berners Bay. Adult females without cubs used space within the 0-100 meter DSC significantly more than adult females with cubs. Adult females not accompanied by cubs used space similarly to dominant adult male bears across all four DSCs. Adult females with cubs used space similarly to subdominant juvenile males and females across all four DSCs during the salmon spawning season.

Coastrange Sculpin and brown bears inhabit a similar geographic area in northwestern North America. Coastrange Sculpin inhabit Pacific coast watersheds from California to the Aleutian Islands. Brown bears inhabit the majority of Alaska, vast areas throughout western Canada, and have scattered populations in the northern Rocky Mountains of the United States. Both of these species have healthy populations in Southeast Alaska, which is home to the most densely populated brown bear population in the world on Admiralty Island. Both species play important roles in the ecosystems of Southeast Alaska and rely heavily on salmon eggs and flesh as a summer food source. These two studies demonstrate the importance of the availability of salmon to the growth and behavior of Coastrange Sculpin and brown bears respectively.

In the last several decades, trends of change in climate and the temporal availability of salmon have become evident throughout Southeast Alaska. Southeast Alaska is expected to have substantial changes in temperature, precipitation patterns (Shanley et al. 2015), and glacial

coverage as a result of climate change (Larsen et al. 2007, Hood and Berner 2009, Fellman et al. 2014). In the next century, mean annual temperature in Southeast Alaska is expected to increase by approximately 1.5-6°C (Shanley et al. 2015). Increasing temperature will increase the maximum summer temperatures in rain-fed systems, but will have a broader impact on precipitation and stream flow patterns. Annual precipitation is expected to increase by 3-18% in Southeast Alaska (Shanley et al. 2015). However, the majority of this will fall as rain rather than snow, which is expected to decrease by as much as 58% in this century in Southeast Alaska (Shanley et al. 2015). Reduced snowfall accumulation at high altitudes and increased winter temperatures will have strong impacts on stream flow patterns in spring and summer. The mean date at which the snowpack has completely melted will become earlier as snowpack decreases and temperature increases. This will lead to decreased summertime flows in streams where discharge relies heavily on high elevation snowpack.

The effects of climate change are most evident in high latitude regions where small increases in temperature lead to major environmental changes relating to the state of frozen water. The climate in Southeast Alaska is mild due to the influence of ocean waters compared to inland areas at the same latitude. Winter temperatures in Southeast Alaska average between -6°C to -1°C from November through March. Increasing winter temperatures due to climate change will increase the number of frost-free days throughout Southeast Alaska. This affects snowpack, ice out dates, and the timing of various biological phenomena. Brown bears spend seven or more months a year in their dens in a state of hibernation. Substantially reduced metabolic rate and inactivity allow bears to survive in winter when food is scarce, while continuous consumption allows bears to put on immense amounts of weight during summer when food is abundant. Warmer winter temperatures and reduced snowfall may decrease the amount of time bears spend in the den, with later den entry and earlier emergence.

Increasing temperatures and reduction in snowpack will also contribute to the recession of glaciers in Southeast Alaska. Glaciers rely on heavy snowfall to continually build or maintain their size. Less snowfall building up on glaciers along with increasing summer temperatures and glacial melt has resulted in the glacial recession observed globally (Oerlemans 1994, Barry 2006, Larsen et al. 2007). In the short term, increasing temperature and glacial melt leads to colder summer temperatures in heavily glacier-fed streams. In the long term, glacial recession will slowly change a watershed from primarily glacier-fed to primarily rain-fed. This change is

accompanied by an increase in summer temperatures and the colonization of stream reaches by species less tolerant of cold and turbid glacial-waters (Milner 1987, Milner and Bailey 1989, Flory and Milner 1999, Milner et al. 2008).

In any population of salmon, some individuals will tend to stray from their natal stream when migrating to spawn (Quinn 1993). These straying individuals are responsible for the colonization of salmon populations in new watersheds. Receding glaciers leave behind stream systems that are colonized over time by a steadily increasing diversity of taxa as temperatures rise, turbidity is reduced, and nutrient inputs increase (Milner et al. 2008). The colonization of bare glacial streams by riparian vegetation and salmon increase the habitat quality for other colonizing organisms. Riparian plants contribute to stream stability and allochthonous inputs, while salmon provide pulses of marine nutrients (Flory and Milner 1999, Milner et al. 2008). Glacial stream colonization by salmon can begin after the peak summer temperatures reach approximately 9°C, with Pink Salmon and Coho Salmon being the first salmon species to colonize (Milner et al. 2008). After successful colonization by salmon, Coastrange Sculpin can colonize streams newly established by glacial recession (Milner et al. 2008).

Climate change and the associated warming of streams in Southeast Alaska may actually benefit some salmon populations during the freshwater period. Streams that are currently too cold to be suitable spawning grounds may become available to colonization by salmon as temperatures increase (Fellman et al. 2014). Warmer temperatures have also been linked to increased productivity of nursery habitats for salmon, which increases growth and survival of fry that spend a portion of their lives rearing in freshwater (Schindler et al. 2005, Mantua et al. 2010, Armstrong et al. 2013). Warming may benefit the freshwater stage of some salmon populations, but the complexity of anadromous salmon life histories and the wide latitudinal gradient that salmon inhabit will likely lead to confounding effects of climate change on salmon productivity and phenology in the future (Crozier et al. 2008, Kovach et al. 2014).

In Southeast Alaska, climate changes have already led to changes in the timing and duration of the spawning migration of several salmon populations. In the last 20 to 50 years many salmon populations have exhibited changes in migration timing with Pink Salmon, Chum Salmon, and Coho Salmon migrating earlier over time and Sockeye Salmon migrating later over time (Kovach et al. 2013, 2015). In addition, salmon populations experiencing the greatest change in migration timing experienced the largest decrease in duration of spawning (Kovach et

al. 2013, 2015). These changes may be leading to decreased phenotypic variation in salmon populations throughout Southeast Alaska (Kovach et al. 2012, 2015). Changes in the spawning migration timing and duration of several salmon species can lead to a substantial reduction in the temporal availability of salmon as a food source in a freshwater system (Kovach et al. 2013).

Reduced temporal availability of salmon will likely negatively impact Coastrange Sculpin and brown bears, but may have confounding effects due to temperature related climate changes. Sculpin may be able to use compensatory growth in order to maximize their consumption of salmon over a shorter period of time, but only if associated water temperatures allow for such growth. Extreme high water temperatures may prevent sculpin from exhibiting compensatory growth due to the increased basal metabolic demands. However, somewhat warmer water temperatures in colder streams may benefit sculpin through increased digestive capacity leading to increased growth. Faster growth might benefit juvenile sculpin survival rates, and increased allocation of energy to gamete formation in adults. The effects of changing salmon migration timing and abundance will affect sculpin populations on a system to system basis due to their limited ability to move between streams to feed on salmon eggs.

Brown bears may be able to move across the landscape in order to track unique salmon runs (Schindler et al. 2013) if the temporal availability of unique salmon runs continues to decrease in Southeast Alaska. However, reduced migration timing may lead to bears enduring longer periods of time without access to a high quality food source, placing added metabolic stress on bears during winter. Compounding those effects, warming air temperatures may lead to bears spending less time hibernating in the den and more time active during the year. Brown bear populations in Southcentral Alaska spend on average 201 days in the winter den with females spending nearly 30 days longer in the den than males (Miller 1990). In Southeast Alaska, bears without cubs spend on average 180 days in the den, and females with cubs spend approximately 46 days longer in the den than males (Schoen et al. 1987). At lower latitudes where winters are shorter, brown bears without cubs remain in the den for an average of only 113-132 days (Judd et al. 1986). Warmer temperatures and shorter winters in Southeast Alaska may lead to a shorter denning period as seen in southern populations. Increasing the period spent outside the den, and decreasing the temporal availability of salmon as a food resource may have negative effects on brown bear condition and survival related to winter denning.

Based on the information gathered from my studies of Coastrange Sculpin and brown bears, and informed by recent work on climate, salmon stocks, and bear populations, I present the following predictions for sculpin and bears if trends in climate and salmon populations continue.

Predictions for Coastrange Sculpin:

1) Sculpin populations that occupy rain-fed drainages with summer temperatures regularly exceeding 20°C are likely to be negatively affected by increasing water temperatures due to the high metabolic costs of homeostasis at these temperatures. If the temporal availability of spawning salmon continues to decrease, sculpin in these warmer streams will experience greater declines in weight and condition during the time when salmon are not present, and may not have a sufficiently long period to catch up using compensatory growth. 2) Sculpin populations that occupy drainages with summer temperatures averaging between 7°C and 12°C may be positively affected by increasing water temperatures due to the increased rate of digestion and assimilation of food items at these temperatures. Decreasing temporal abundance of salmon will reduce food availability, but through increased digestion and the use of compensatory growth, sculpin in these systems could maintain or increase their annual growth rates. 3) Sculpin populations that occupy predominantly glacier-fed drainages where water temperatures are relatively constant throughout the year, may be positively affected by climate warming through increased digestion and the increase in availability of prey items. As glaciers recede and rain water contributes more to the total discharge, warmer water temperatures could allow for the increased production of biofilm, macroinvertebrates, and the presence of salmon. New thermal habitat may allow the colonization of new spawning grounds by salmon, providing food and nutrient subsidies for the stream system. The increased abundance of prey, and slightly warmer temperatures could allow sculpin in these drainages to exceed their previous annual growth rates, and use compensatory growth to endure periods of low food availability.

Predictions for brown bears:

1) Warmer environmental temperatures, especially during the winter months, may lead to delayed entry or early exit of the den by brown bears. A longer annual duration outside the den will increase the annual caloric budget of bears due to extended periods of activity. 2) Compounding this issue, decreased salmon spatial or temporal availability in Berners Bay as a result of changes in migration timing might negatively influence brown bears, which rely almost

entirely on salmon during late summer and fall. Earlier and shorter spawning migrations mean bears may be active for longer periods of the summer without a high quality food source to put on fat reserves. However, warming temperatures and glacial recession in Berners Bay may also allow for the colonization of new thermal spawning habitat by salmon, which would benefit bears. 3) Construction of the proposed Juneau Access Improvements Project road might cause bears to avoid or abandon several of the unique salmon fishing locations along the coastline in Berners Bay. This could lead to increased bear congregations at more remote fishing locations, potentially influencing social interactions at these sites. Increased human and bear conflict as a result of the road would most likely have negative effects on the brown bear population in Berners Bay.

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